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# Lophophaeninae (Radiolaria) from the Upper Oligocene to Lower Miocene and Intrageneric Variation in Their Internal Skeletal Structures

Satoshi FUNAKAWA*

(with 11 Figures and 10 Plates)

**Abstract**

The Upper Oligocene to Lower Miocene Kawakami Group is distributed on the western side of the Shiranuka Hills region, eastern Hokkaido, Japan. This group is composed of marine sediments that are characterized by the intercalation of abundant biosiliceous and tuffaceous layers. From several calcareous nodules included in biosiliceous beds, well preserved radiolarian remains occur. This paper describes 11 new species of Lophophaeninae.

In addition to the Late Oligocene to Early Miocene Lophophaeninae, the present author examined the internal skeletal structures of Lophophaeninae from the Upper Miocene and of recent plankton samples. As a result of these examinations, the intrageneric variations in internal skeletal structures are recognized in several genera. It is considered that these intrageneric variations in internal skeletal structure represent one aspect of their evolutionary lineage. This paper describes the intrageneric variations of some Lophophaeninae and discusses them in the suprageneric classification.

**Key Words:** Late Oligocene to Early Miocene, Lophophaeninae, internal skeletal structure, intrageneric variation, suprageneric classification

## Introduction

Paleogene plagiacanthids (Radiolaria) occur from deep sea sediments of the equatorial to high latitudinal region. From DSDP (Deep Sea Drilling Project) and ODP (Ocean Drilling Program) cores, many investigators have reported Oligocene plagiacanthids : CHEN (1975), PETRUSHEVSKAYA (1975), ABELMANN (1990), CAULET (1991) and TAKEMURA (1992) from the Antarctic Sea; BJØRKLUND (1976) from the Norwegian Sea; SANFILIPPO and RIEDEL (1973) from the Gulf of Mexico and NISHIMURA (1992) from northwest Atlantic. However Oligocene plagiacanthids are not yet reported from the central and north Pacific.

The Upper Oligocene to Lower Miocene strata of eastern Hokkaido yield well preserved radiolarian remains. It is important to study Oligocene radiolarians in this region for the paleobiogeography and evolutions of some taxa. The present author describes 11 new species of Lophophaeninae obtained from these strata.

As a tool for classification of Nassellaria, their internal skeletal structures have been

* Department of Geosciences, Faculty of Science, Osaka City University, Sugimoto 3-3-138, Sumiyoshi-ku, Osaka 558, Japan

examined by many investigators (RIEDEL, 1967, 1971; PETRUSHEVSKAYA, 1971a, 1971b, 1975, 1981; TAKEMURA, 1986; NISHIMURA, 1990; SUGIYAMA, 1993) and on the basis of these examinations, they presented many classificatory schemes. Recently, FUNAKAWA (1994) presented the internal skeletal structures of plagiacanthids and indicated that some subfamilies of PETRUSHEVSKAYA (1971b) are composed of several groups that have different skeletal structures. In this paper, the author attempts to apply the internal skeletal structure as a tool for explanation of evolutionary lineages. Application of this factor for the phylogeny of Lophophaeninae is a most suitable approach for the following reasons : (1) internal skeletal structure is formed during early ontogeny (SWANBERG and BJØRKLUND, 1987 ; NISHIMURA, 1990); (2) it is easy to observe the internal skeletal structure of Lophophaeninae because most internal skeletal elements are not buried in the shell; (3) the shell shows highly varied morphologies and the basic external skeletal structure is controlled by the internal skeletal structure (FUNAKAWA, 1994).

In this paper, the intrageneric variations of internal skeletal structure in several genera of Lophophaeninae are described. Moreover the author indicates the significance of intrageneric variations in Lophophaeninae for their suprageneric classification.

## Geologic setting and materials

The Kawakami Group (MITANI *et al.*, 1959) is composed of marine sediments and is distributed in the Hombetsu, Morawan and Kamiashoro regions, eastern Hokkaido, Japan (Fig. 1). From the Kawakami Group, some Oligocene and Early Miocene fossils have been reported; also some mammals, Desmostylia and Cetacea (MATSUI and GANZAWA, 1987), some mollusks and benthic foraminiferas (e.g. INOUE and SUZUKI, 1962; MIZUNO, 1964; MIZUNO *et al.*, 1969), and diatoms (SAITO *et al.*, 1988).

The Kawakami group is characterized by large amounts of biosiliceous and tuffaceous sediments. In the Morawan region, this Group is widely distributed and is subdivided into three formations (Fig. 2), namely the Hombetsuzawa, Morawan and Kiroro Formations in ascending order (INOUE and SUZUKI, 1962). The general geologic structure in this region is controlled by the Kamirawan Anticlinorium and the Morawan Synclinorium (KIMURA, 1979). In this paper, the stratigraphic subdivision follows that of INOUE and SUZUKI (1962). The Hombetsuzawa Formation is characterized by siliceous mudstone and is exposed near the junction of the Morawan-gawa and Rawan-gawa Rivers, at the axis of the Kamirawan Anticlinorium. The Morawan Formation, characterized by large amounts of siliceous mudstones and tuffaceous rocks, is distributed around the axis of the Kamirawan Anticlinorium and is subdivided into four members : the lower platy shale, the Kamirawan sandstone, the middle hard shale and the upper tuffaceous mudstone members. The Kiroro Formation, characterized by the non-siliceous rocks, is distributed around the axis of the Morawan Synclinorium and is subdivided into two members : the lower sandstone and the upper siltstone members.

The depositional age of this group is suggested by K-Ar and fission track dating and occurrences of diatom fossils (Fig. 3). MATSUI and GANZAWA (1987) presented the

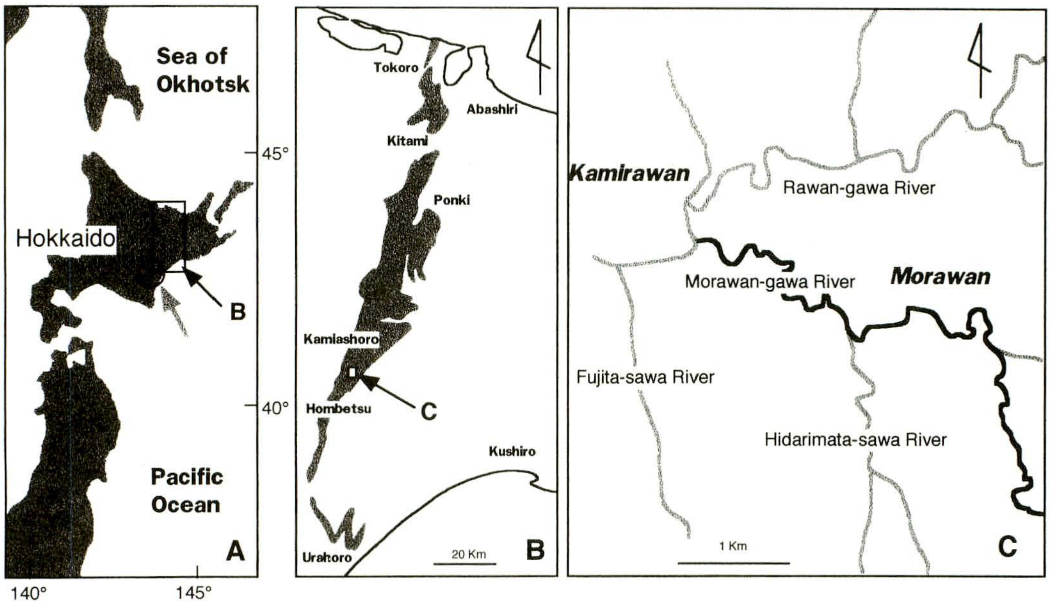



Fig. 1. Index maps showing study area. **A** indicates northwestern Japan around Hokkaido, gray arrow shows Toyokoro Hills region; **B** shows the distributional areas (gray area) of the Upper Oligocene to Lower Miocene strata (after MATSUI and GANZAWA, 1987); **C** shows the river system around the Morawan-gawa River. In Figure **C**, black line indicates the study route and italic letters are place names.

depositional ages of some members of the Kawakami Group. SAITO *et al.* (1988) reported some diatoms from the lower platy shale member of the Morawan Formation as indicating a Late Oligocene assemblage. From the upper siltstone member of the Kiroro Formation, a diatom species, *Thalassiosira fraga*, occurs without occurrence of *Actinocyclas ingens* (ARIGA, in prep.). This result indicates that the age of the upper limit of this member is between 19.5 Ma and 16.8 Ma (AKIBA, 1986). These ages suggest that the Kawakami Group was deposited during Late Oligocene to Early Miocene time.

Along the Morawan-gawa River route, members of the Kawakami Group are well exposed. Siliceous mudstone beds of the Morawan Formation and siltstone beds of the Kiroro Formation yield several calcareous nodules that contain well preserved radiolarian remains. Calcareous nodules from the Morawan Formation are large and discoidal in shape (50 to 200 cm in diameter and 10 to 50 cm in thickness); and those from the Kiroro Formation are spherical or irregularly shaped and are smaller than those from the Morawan Formation, being 2 to 30 cm in diameter. The present author studied radiolarian remains from these seven calcareous nodules of four horizons (Figs. 2, 3).

The chronological estimation of each sample horizon is as follows (Fig. 3) : 90081302, 90081501 and 90081306 are between $29.3 \pm 3.3$ Ma and $27.4 \pm 1.5$ Ma, especially 90081306, which is just before $27.4 \pm 1.5$ Ma; 90081402 is between $27.4 \pm 1.5$ Ma and $23.8 \pm 2.0$ Ma; MW-125, -120 and -118 are younger than 19.5 Ma and older than 16.8 Ma.

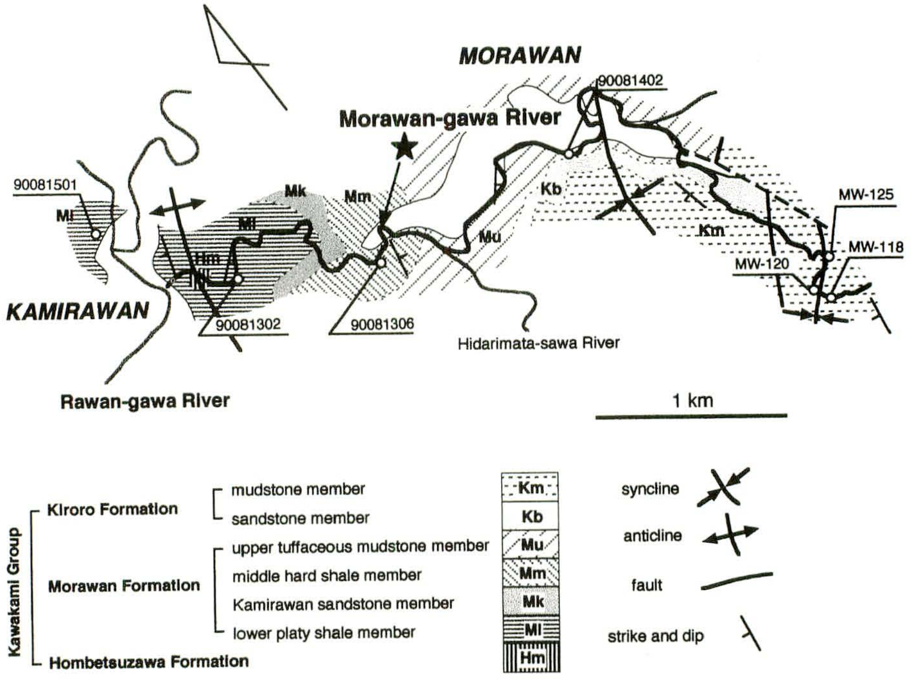



Fig. 2. Locality of each sample in the Morawan-gawa River Route. Stratigraphy and geological structure are from INOUE and SUZUKI (1962). Black star indicates the locality of rock samples for K-Ar dating by MATSUI and GANZAWA (1987).

Preparation of radiolarian specimens : Calcareous nodules are immersed in a solution of hydrochloric acid, and the residue is then cleaned by boiling in a solution of hydrogen peroxide. Radiolarian specimens are observed under the Scanning Electron Microscope (SEM) and the optical microscope. Identification of radiolarians is done under the SEM, with the observation of fine skeletal structures. Amounts of each taxon are estimated under the transmitted optical microscope.

In addition, the present author examined the Late Miocene and recent Lophophaeninae to investigate internal skeletal structure. The Late Miocene sample, 91092607, is from the Taiki Formation, eastern Hokkaido (FUNAKAWA, 1993, 1994); its locality and horizon refer to FUNAKAWA (1994; Figs. 2, 3). Recent plankton specimens were collected at Leg 1, Station 10, off the coast of Shirahama, the Kii Peninsula, southwest Japan (Fig. 4).

Depository of the type specimens is the Department of Geosciences, Faculty of Science, Osaka City University (OCU).

## Notes for terminology of internal skeletal structure

Skeletal terms follow PETRUSHEVSKAYA (1968) and DUMITRICA (1991) : **MB** (median-bar), **A** (apical spine), **D** (dorsal spine), **V** (ventral spine), **L** (right and left

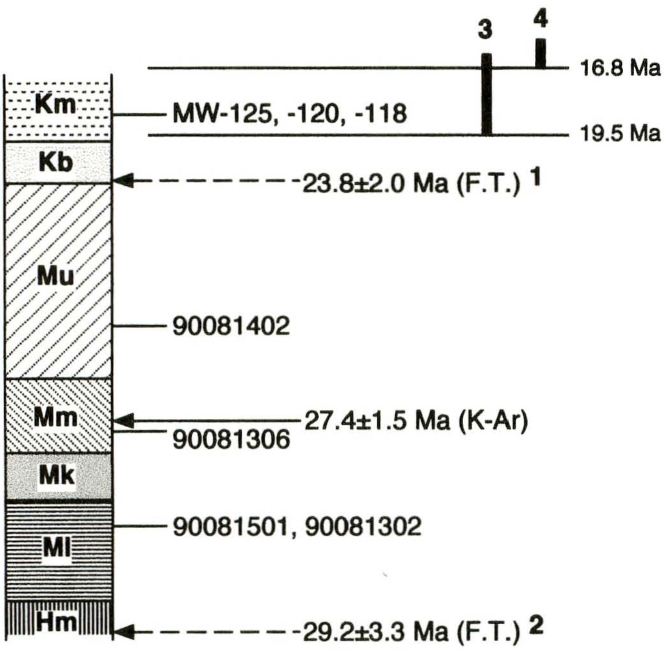



Fig. 3. Conceptual column showing the horizons of each sample. All abbreviations refer to those in Figure 2. Isotopic ages are from MATSUI and GANZAWA (1988). Solid arrow shows the datum obtained at the Morawan-gawa River Route. Broken arrows show data obtained at other areas; **1** is obtained from the base of the Tsubetsu Formation, which corresponds to the Kiroro Formation in the Tsubetsu area; **2** is from the base of the Hombetsuzawa Formation in the Hombetsu area. Diatom occurrences are after ARIGA (in prep.); **3** is *Thalassiosira fraga*, **4** is *Actinocyclus ingens*. The age estimations of the first appearances of these two diatoms are from AKIBA (1986).

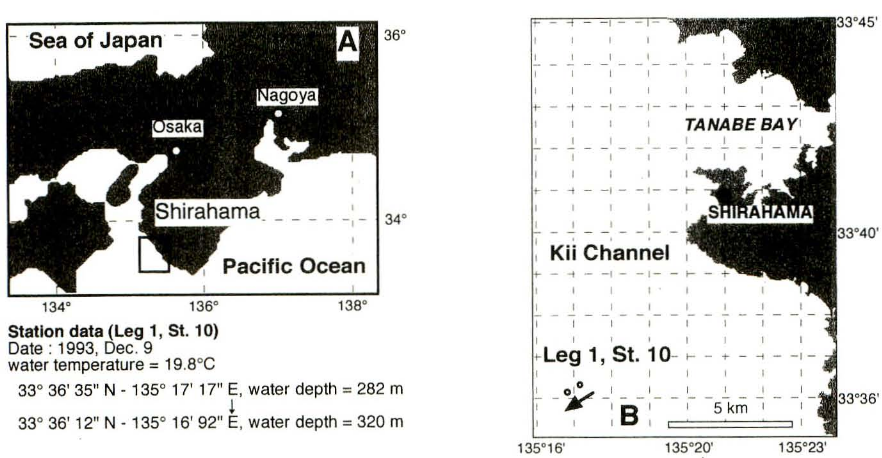



Fig. 4. Index map showing locality of sampling station of recent plankton specimens.

lateral spines) and **l** (right and left secondary lateral spines); notation of connecting arch is two abbreviations of internal elements connecting together (i.e. **AL** is an arch connecting **A** and **L**, **D-AL** is an arch connecting **D** and **AL**, **A-(D-AL)** is an arch connecting **A** and **D-AL**). In this paper, spines and ribs extending from internal spicules are included in internal skeletal structure : **A** forms an apical rib in the shell wall and an apical horn outside the shell; **V** forms a ventral rib in the shell wall and a ventral horn outside the shell; **D** forms a dorsal rib in the shell wall and a foot outside the shell; two **L** form two lateral ribs in the shell wall and two feet outside the shell. **L-R** and **A′** were defined by SUGIYAMA (1993); the former is applied for the skeleton where **AL** converges with **VL** or **LL** and the latter is for the skeleton extending dorsally from **A** at near the junction of **A** and **AL**. In addition, following single term, **L-Rd**, is defined for some genera having dorsal side connecting arches such as **AL-AL**, **D-AL** or **A′-AL**; **L-Rd** is a part of **AL** between **L** and the junction of **AL** and **AL-AL** (or **D-AL** or **A′-AL**).

In addition, some terms defined in SUGIYAMA (1993) are applied to *Pseudocubus* and *Steganocubus* : **l′** extends laterally from **AL**; **l″** extends upwardly from **AL** at the same point of the intersection of **AL** and **l′**; **V′** extends laterally from **LL** or the junction of **V** and **VL**; **V″** extends upwardly from **LL** or the junction of **V** and **VL**. **PR** and **DR** are subdivided into some connecting arches, the former is into two **AL** and one **LL** and the latter is into two **Al″** and two **V″l″**.

## Taxonomic descriptions

Order Polycystina EHRENBERG, 1838, emend. RIEDEL, 1967

Suborder Nassellaria EHRENBERG, 1875

Family Plagiacanthidae HERTWIG, 1879, emend. PETRUSHEVSKAYA, 1971a

Subfamily Lophophaeninae HAECKEL, 1881, emend. PETRUSHEVSKAYA, 1971b

### Genus *Amphiplecta* HAECKEL, 1881, emend. PETRUSHEVSKAYA, 1971b

*Type species* : *Amphiplecta acrostoma* HAECKEL, 1887.

***Remarks*** : The generic concept follows PETRUSHEVSKAYA (1971b) and FUNAKAWA (1994). The following species from the Kawakami Group has different structures from type species of this genus. The problem of generic assignment is described in the following specific remarks. Schematic diagrams of the internal skeletal structure of the following one species are shown in Fig. 5.

### *Amphiplecta tripleura* FUNAKAWA, sp. nov.

Plate 1, figs. 1a-3b

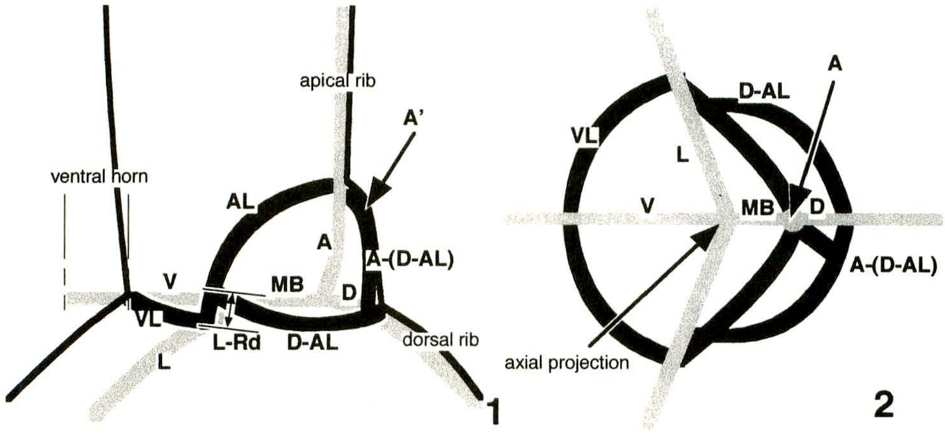



Fig. 5. Schematic diagrams of internal skeletal structure of *Amphiplecta tripleura* FUNAKAWA, sp. nov. : **1** is left lateral view; **2** is basal view. Gray elements are internal spicules and black elements are connecting arches. All abbreviations refer to the text.

***Type specimen*** : Holotype is OCU CR-0007.

*Amphiplecta* sp.; Petrushevskaya, 1971b, pl. 54, fig. 1.

***Description*** : Shell is composed of two segments. Internal skeletal structure is composed of **A, MB, D,** two **L, V,** two **AL,** two **D-AL,** two **VL** and **A′**. **A′** forms **A-(D-AL)**. **L-R** is absent. **V** is thinner than the other internal spicules. Two **L-Rd** are short. **A** forms a long apical rib and a short apical horn. **V** forms a ventral horn. **D** and two **L** are well developed and form three dorsal and lateral ribs. First segment is cylindrical with long and distinct apical rib extending to apical horn. Apical horn is not bladed, short and narrow. Ventral horn is not bladed and extends obliquely upward. Its length is one to two times that of apical horn. **A′** is well-developed and diverges from **A** at the junction of **A** and **AL**. **A′** forms **A-(D-AL)**; it shifts a little to right or left side from the plane of bilateral symmetry and so it connects with **D-AL** at near the junction with **D** (Plate 1, figs. 1c, 3b). Axial projection is distinct. Pores in the first segment are circular to subcircular and are not aligned. Pore bars are very thin. First segment is distinguished from second segment by two **VL**, a part of both two **AL** and two **D-AL**. Two **D-AL** are distinct. On the underside of both **L** and **D**, there are two or three small and irregularly arranged projections (Plate 1, figs. 1b, 1c). On the lateral side of **A**, there are one to two pairs of trigonal projections (Plate 1, fig. 1c). There are a pair of lateral projections (**l** ?) on **D** that are trigonal to thorny (Plate 1, figs. 1b, 2). Second segment is expanded horizontally. In most specimens, lateral and dorsal ribs are indistinct. Three feet are not developed. Pores in the second segment are circular to subcircular and not aligned and pore bars are very thin. Distal end of the second segment is fully open.

***Dimensions*** (in $\mu$m) : Measurements are based on 19 specimens. Outside diameter of first segment is 45–92 (average is 59), inside width between each **D-AL** is 56–74 (64) and inside depth between **A-(D-AL)** and **VL** is 44–58 (51), maximum diameter of second segment is 77–136 (111). Total height of shell is 83–168 (106).

***Remarks*** : This species has different internal skeletal structure from *A. acrostoma* HAECKEL (FUNAKAWA, 1994, p. 462), this species has **D-AL** at the dorsal to lateral side of shell but *A. acrostoma* has no **D-AL**.

***Etymology*** : The specific name means "three ribs" in Latin.

***Occurrences*** : MW-125, -120 and -118. Few in abundance.

***Stratigraphic notes*** : Lower Miocene.

### Genus *Ceratocyrtis* BUTSCHLI, 1882, emend. PETRUSHEVSKAYA, 1971b

*Type species* : *Cornutella cucullaris* EHRENBERG, 1873 (designated by PTRUSHEVSKAYA, 1971b).

***Remarks*** : **A** forms an apical rib in the shell wall and an apical horn. **V** forms a ventral horn. **D** and two **L** are poorly developed and form indistinct lateral and dorsal ribs. **A′** is poorly developed and is hardly recognized. Feet are poorly developed. Schematic diagrams of the internal skeletal structure of this genus are shown in Fig. 6.

### *Ceratocyrtis morawanensis* FUNAKAWA, sp. nov.

Plate 1, figs. 4–5b

***Type specimen*** : Holotype is OCU CR-0008.

***Description*** : Shell is composed of two segment. First segment is hemi- to

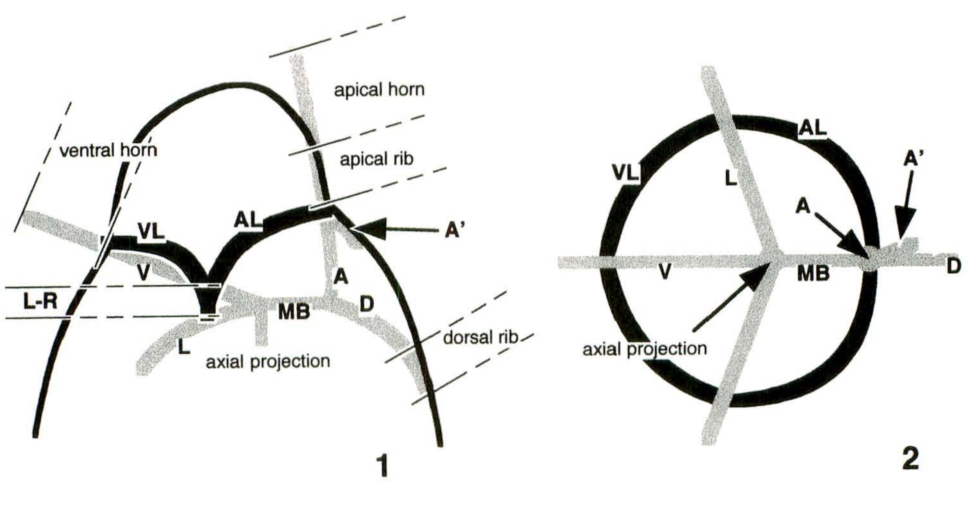



Fig. 6. Schematic diagrams of internal skeletal structure of *Ceratocyrtis* and *Pseudodictyophimus* : **1** is left lateral view; **2** is basal view. Gray elements are internal spicules and black elements are connecting arches. All abbreviations refer to the text.

sub-spherical with very stout apical horn. Apical horn is three-bladed and its length is about two times the height of the first segment. Pores in the first segment are small, subcircular and randomly arranged. Ventral horn is robust, three-bladed and shorter and narrower than the apical horn. **A′** is hardly recognized and diverges from **A** at the junction of **A** and **AL.** Second segment is truncated conical to bell-shaped. In some specimens, **D** and two **L** form very fine three lateral feet on the upper part of the second segment. Pores in the second segment are circular to subcircular, larger than those in the first segment and aligned vaguely in longitudinal rows. Distal end of the second segment is fully open, with well-developed teeth.

***Dimensions*** (in $\mu$m) : Measurements are based on 10 specimens. Length of apical horn is 56–88 (75), ventral horn is 38–62 (51). Outside diameter of first segment (not including apical and ventral horns) is 32–48 (43), second segment (not including feet) is 101–151 (128). Height of first segment (not including apical horn) is 31–43 (36), total height of shell (not including apical horn and distal teeth) is 102–149 (127).

***Remarks*** : This species is distinguished from *C. histricosus* (JORGENSEN) by the stouter apical and ventral horns and vaguely aligned pores in the second segment. This species resembles *Lophophaena* (?) *thaumasia* CAULET but is distinguished by the longer apical and ventral horns and larger shell.

***Etymology*** : The specific name is derived from occurrence place name, "Morawan" in eastern Hokkaido, Japan.

***Occurrences*** : 90081302, 90081501 and 90081306. Few to common in abundance.

***Stratigraphic notes*** : Upper Oligocene.

## Genus *Peridium* HAECKEL, 1881

*Type species* : *Peridium spinipes* HAECKEL, 1887.

***Remarks*** : **A** forms an apical rib and, in some species, forms an apical horn. **V** forms a ventral horn or a ventral rib. **D** and two **L** do not form dorsal and lateral ribs. First segment occupies large amount of shell. Schematic diagrams of the internal skeletal structure of the following two species are shown in Fig. 7.

### *Peridium sphaerum* FUNAKAWA, sp. nov.

Plate 2, figs. 1a-4b

(?) Plagoniid, gen. et sp. indet.; TAKEMURA, 1992, p. 744, pl. 1, fig. 10.

***Type specimens*** : Holotype is OCU CR-0011; paratypes are OCU CR-0012 and -0013.

***Description*** : Shell is composed of two segments. The upper part of the first segment is spherical and the lower part is funnel-shaped. **A** is present at only the lower part of the first segment as apical rib. Apical horn is not recognized. **V** extends obliquely upward at an acute angle and extends in the shell wall as a ventral rib at the lower part of the first segment. **A′** is absent. In some specimens the apex of the first

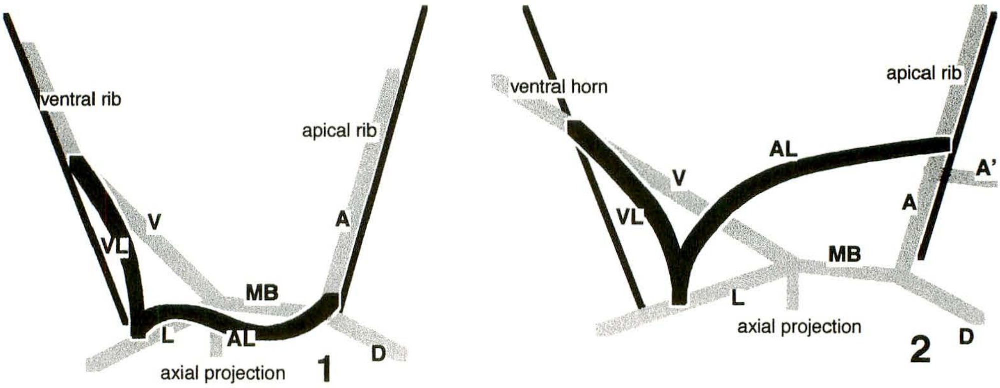



Fig. 7. Schematic diagrams of internal skeletal structure of *Peridium*. These are left lateral views. **1** is *P. sphaerum* FUNAKAWA, sp. nov.; the interval of **A** between the junction of **A** and **MB** and that of **A** and **AL** is very short. **2** is *P. infundibuliforme* FUNAKAWA, sp. nov.; **A** is longer than that of *P. sphaerum*. All abbreviations refer to the text.

segment is open (Plate 2, fig. 2a). Pores in the first segment are subcircular to elliptical and are not aligned. Thickness of pore bars is variable. Axial projection is present. **AL** diverges from **A** at just above the junction of **MB, A** and **D,** and so the lower part of **A** between the junction of **A** and **MB** and that of **A** and **AL** is very short and hardly recognized. Second segment is formed by only **D** and two **L**. Below these spicules, shell wall is not formed.

***Dimensions*** (in $\mu$m) : Measurements are based on 19 specimens. Maximum diameter of first segment is 62–101 (79), width between both **AL** is 22–28 (24), depth between **AL** and **VL** is 18–25 (21). Total height of shell is 88–141 (110).

***Remarks*** : In most specimens, **AL** seems **l** and **Ll** because the interval of **A** between the junction of **A** and **MB** and that of **A** and **AL** is very short. TAKEMURA (1992) reported a form, Plagoniid gen. et sp. indet. from the Upper Oligocene of Southern Indian Ocean (ODP Leg 120, Site 748B). TAKEMURA's form is approximately similar to this species except for the shorter height of shell than the present species. It is considered that this species has a close relation to TAKEMURA's form in phylogeny because of the similarity of shell morphology between them. This species is distinguished from *Peridium spinipes* HAECKEL by the large first segment. This species is distinguished from *Cryptogyrus trachylobus* SUGIYAMA by the larger shell.

***Etymology*** : The specific name means "sphere" in Latin.

***Occurrences*** : 90081302, 90081501 and 90081306. Rare to few in abundance.

***Stratigraphic notes*** : Upper Oligocene.

### ***Peridium infundibuliforme*** **FUNAKAWA, sp. nov.**

Plate 3, figs. 1a-4

***Type specimens*** : Holotype is OCU CR-0014; paratype is OCU CR-0015.

***Description*** : Shell is composed of two segments. First segment is subdivided into the upper and lower parts; the upper part is ellipsoidal and the lower part is funnel-shaped. In some specimens, the apex of the first segment is open and the whole shell of the first segment is funnel-shaped (Plate 3, fig. 4). Boundary between the upper and lower parts is indistinct. In the lower part of the first segment, there are some short spines that diverge and connect each other. Pores in the first segment are circular to subcircular and not aligned, and those in the lower part are larger than those in the upper part. **A** forms a distinct apical rib and a very small apical horn (Plate 3, figs. 3a, 4). **V** forms a ventral horn. Ventral rib is absent. **A′** is spiny and diverges from **A** at the lower horizon than the junction of **A** and **AL** (Plate 3, figs. 1b, 2a). Axial projection is distinct. **D** has one projection on the underside of it and has a pair of lateral projections (**l** ?) that are trigonal to spiny (Plate 3, figs. 1c, 3c). Second segment is formed by only **D** and two **L**. Below these spicules the shell wall is not formed.

***Dimensions*** (in $\mu$m) : Measurements are based on eight specimens. Maximum diameter of first segment is 59–75 (70), width between both **AL** is 22–27 (25) and depth between **AL** and **VL** is 23–26 (24). Total height of shell is 84–111 (102).

***Remarks*** : This species is distinguished from *Peridium sphaerum* FUNAKAWA by the longer interval of **A** between the junction of **A** and **MB** and that of **A** and **AL**, and distinct **A′** and ventral horn; and from *P. spinipes* by numerous pores and thickened pore bars in the first segment.

***Etymology*** : The specific name means "funnel-shaped" in Latin.

***Occurrences*** : MW-125, -120 and -118.

***Stratigraphic notes*** : Lower Miocene.

### Genus *Pseudocubus* HAECKEL, 1887, sensu SUGIYAMA, 1993

*Type species* : *Pseudocubus obeliscus* **HAECKEL**, 1887, p. 1010, pl. 94, fig. 11.

***Remarks*** : The generic concept and assignment of subfamily follow SUGIYAMA (1993). Schematic diagrams of the internal skeletal structure of the following two species are shown in Fig. 8.

#### *Pseudocubus obeliscus* HAECKEL

Plate 4, figs. 2a-3b

*Pseudocubus obeliscus* HAECKEL, 1887, p. 1010, pl. 94, fig. 11; PETRUSHEVSKAYA, 1971b, p. 150. pl. 76, figs. 1–6.

*Plectophora triacantha* POPOFSKY, 1908, p. 262, pl. 29, fig. 1, pl. 30, fig. 1.

*Obeliscus pseudocuboides* POPOFSKY, 1913, p. 280, pl. 29, figs. 4, 5.

***Remarks*** : Internal skeletal structure is composed of **MB, A, D,** two **L, A′, V′, V″** two **l′**, two **l″**, two **AL, LL,** two **Al″** and two **V″l″** (Fig. 10). **A′, V′** and two **l′** extend horizontally to oblique downwardly. **V″** and two **l″** extend upwardly. **L-R** is very short and is hardly recognized. **A′** is well-developed and diverges from **A** at the junction

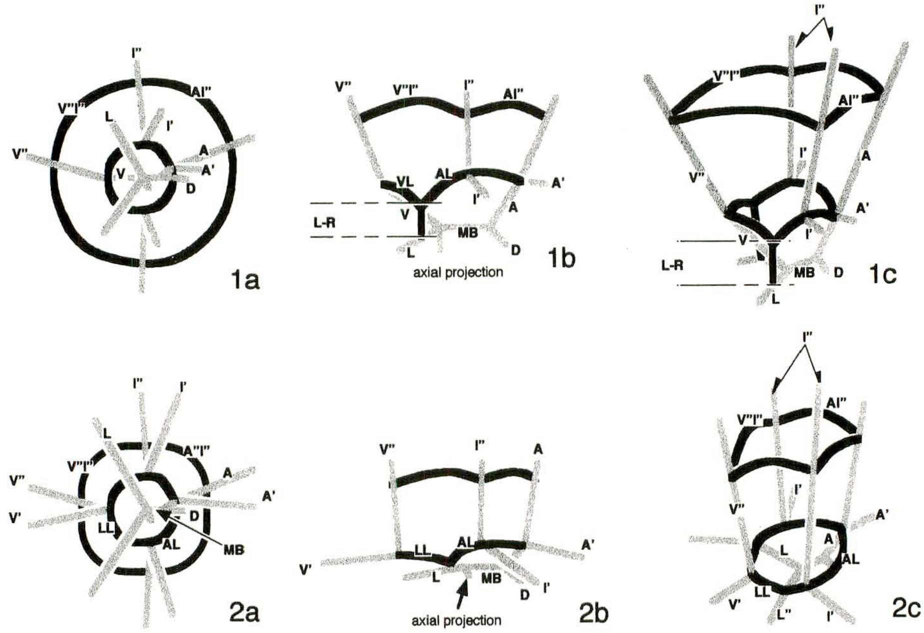



Fig. 8. Schematic diagrams for the internal skeletal structure of *Pseudocubus*. **1** : *P. praeobeliscus* FUNAKAWA, sp. nov.; **2** : *P. obeliscus* HAECKEL. **a** : basal view; **b** : enlargement of left lateral view; **c** : obliquely apical to left lateral view. All abbreviations refer to the text.

of **A** and **AL**. Axial projection is distinct. **D** is very thin with a pair of lateral projections (**l** ?). **MB, D,** lower part of **A** between the junction of **A, D** and **MB** and that of **A** and **AL,** basal part of **L** between the junction of **L** and **MB** and that of **L, AL** and **LL** are circular in section and other spicules are three-bladed in section. Two **L, A′, V′** and two **l′** diverge at near their terminal. Several spicules extend from junctions of **A** and **Al″**, **l″** and **Al″**, and **V″** and **V″l″**, that are three-bladed in section and have two to four radial spicules at the near terminal.

This species was described by HAECKEL (1887) from the surface sediment collected in the Central Pacific, and was reported by POPOFSKY (1908, 1913) from the Antarctic sea, although different specific names were adopted. PETRUSHEVSKAYA (1971b) described *P. obeliscus* having stable **V** from the recent plankton samples of the Indian and Pacific Oceans (PETRUSHEVSKAYA, 1971b, Fig. 76; 4, 6). The very short **L-R** and the presence of **V″** are specific characters of *P. obeliscus*. POPOFSKY's sketches and the present specimens do not have **V** and so the presence of **V** is considered as an intraspecific variation of this species.

Internal skeletal structure of this species is similar to that of *Pseudocubus warreni* GOLL. The present species does not have shell wall and is distinguished from *P. warreni* by this character.

***Dimensions*** (in $\mu$m) : Measurements are based on 15 specimens. Depth between **A** and **V″** at the horizon of **Al″** and **V″l″** is 44–57 (50), width between both **AL** is 21–26 (24), maximum diameter of skeleton is 98–184 (134). Height from **MB** to **Al″** or **V″l″** is 38–51 (44), total height of skeleton is 61–144 (95).

***Occurrence*** : Recent plankton samples.

### *Pseudocubus praeobeliscus* FUNAKAWA, sp. nov.

Plate 4, figs. 1a-1d; Plate 5, figs. 1a-3c

*Pseudocubus obeliscus* HAECKEL; SUGIYAMA, 1993, p. 51, Figures 7–8.

***Type specimens*** : Holotype is OCU CR-0016; paratypes are OCU CR-0017 and -0018.

***Description*** : Internal skeletal structure is composed of **MB, A, D,** two **L, V, V″,** two **l′**, two **l″**, two **AL,** two **VL,** two **Al″** and two **V″l″** (Fig. 10). Most specimens have **A′**. **A′** and two **l′** extend horizontally to oblique downwardly. **V** and **V″** are completely continuous. **V″** and two **l″** extend upwardly. **L-R** is distinct. In most specimens, **A′** is well-developed and diverges from **A** at the junction of **A** and **AL.** Axial projection is distinct. **A** has a pair of lateral projections and in some specimens they extend and connect with **AL** (Plate 5, fig. 1c). **D** is very thin with a pair of lateral projections (**l** ?) and a downward projection that is small and spiny. **L** has one to three downward projections. **MB, D,** basal part of **A,** basal part of **L** between the junction of **L** and **MB** and that of **L, AL** and **VL,** and a part of **AL** (**L-R**) are circular in section and other spicules are three-bladed in section. The top of the apex of the skeleton has some spines randomly connecting with each other and forming a rough meshwork (Plate 5, fig. 2b). The whole skeleton is inverted quadrangular pyramidal shaped, with four props, **A, V″** and two **l″**.

***Dimensions*** (in $\mu$m) : Measurements are based on 14 specimens. Depth between **A** and **V″** at the horizon of **Al″** and **V″l″** is 53–69 (60), width between both **AL** is 24–31 (27). Height from **MB** to **Al″** or **V″l″** is 42–64 (51), total height of skeleton is 76–108 (87).

***Remarks*** : This species has an almost similar skeleton to *Pseudocubus obeliscus* HAECKEL, except for the following three skeletal characters : 1) the presence of **V** (Plate 4, fig. 2b); 2) recognizable **L-R** (Plate 4, figs. 2b, 3b); 3) the absence of **V″** (Plate 4, fig. 2b). This species is distinguished from *P. obeliscus* by the above-mentioned characters. It is distinguished from *P. warreni* GOLL by the absence of shell wall and the longer **L-R.**

SUGIYAMA (1993) reported *P. obeliscus* from the Lower Miocene, with description of its fine skeletal structures. It is obvious that SUGIYAMA's species is not *P. obeliscus* but *P. praeobeliscus.*

***Occurrences*** : MW-125, -120 and -118.

***Stratigraphic notes*** : The first appearance horizon of this species is in the Lower Miocene. Last occurrence horizon is unknown, but the author has confirmed the occurrence from the Upper Miocene that is correlated with the *Denticulopsis katayamae* zone.

### Genus *Pseudodictyophimus* PETRUSHEVSKAYA, 1971b

*Type species* : *Dictyophimus gracilipes* BAILEY, 1856.

***Remarks*** : **A** forms an apical rib in the shell wall of the first segment and extends outside the shell as an apical horn. **V** forms a ventral horn and does not form a ventral rib. **D** and two **L** are well developed and form lateral and dorsal ribs in the shell wall of the second segment and extend outside the shell as distinct feet. In most species, **A′** is poorly developed and is hardly recognized. Schematic diagrams of the internal skeletal structure of this genus are shown in Fig. 6.

### *Pseudodictyophimus gracilipes* (BAILEY)

Plate 6, figs. 1–2c

*Dictyophimus gracilipes* BAILEY, 1856, p. 4, pl. 1, fig. 8.

*Pseudodictyophimus gracilipes* (BAILEY); PETRUSHEVSKAYA, 1971b, pl. 48, figs. 1,3–6; pl. 49, figs. 6–7; FUNAKAWA, 1994, p. 472, Figures 12, 1a-b.

*Pseudodictyophimus* sp.; NISHIMURA, 1990, p. 96, pl. 18, figs. 5a-b (not pl. 16, figs. 9–10b).

***Remarks*** : The Late Oligocene to Early Miocene specimens have shallow furrows along **AL** and **VL.** **A′** is distinct in some Late Oligocene specimens (Plate 6, fig. 2c). An apical horn has variable length.

***Dimensions*** (in $\mu$m) : Measurements are based on 23 specimens. Length of apical horn is 9–43 (23), ventral horn is 9–36 (17). Maximum diameter of first segment is 28–51 (35), second segment is 56–109 (75). Height of first segment (not including apical and ventral horns) is 19–34 (28), total height of the shell (not including feet, distal teeth, apical and ventral horns) is 41–97 (61).

***Occurrences*** : All samples. Rare to few.

***Stratigraphic notes*** : The first appearance horizon of this species may be lower than the Upper Oligocene.

### *Pseudodictyophimus leptoretis* FUNAKAWA, sp. nov.

Plate 6, figs. 3a-4b; Plate 7, figs. 1a-1c

***Type specimens*** : Holotype is OCU CR-0019; paratype is OCU CR-0020.

***Description*** : Shell is composed of two segments. Shell wall is thin, with numerous fine pores. Lateral sight of the first segment is fan-shaped because of the acute angle between **AL** and **VL.** Apical rib is poorly developed. Apical and ventral horns are three-bladed; they extend obliquely upward and are approximately the same length to the height of the first segment. **A′** extends downwardly and diverges from **A** at the lower horizon than the junction of **A** and **AL** (Plate 6, figs. 3c, 4b; Plate 7, fig. 1c). Pores in the first segment are circular, randomly arranged and are small. Axial projection is distinct. There are one to three distinct projections on the underside of both **L** (Plate 6, figs. 3c, 4b; Plate 7, fig. 1b). A pair of lateral trigonal projections (**l** ?) is present on **D** (Plate 6, figs. 3c, 4b). **V** has two or three trigonal to spiny projections (Plate 6, figs. 3c, 4b; Plate 7, fig. 1c) that connect with the shell wall in some specimens (Plate 6, figs. 3b, 4b). In some specimens, **VL** are hardly recognized (Plate 7, fig. 1b). Furrows between two segments along two **AL** and two **VL** are indistinct. Second segment is subdivided into upper and lower parts; the upper part is bell-shaped, with distinct lateral and dorsal ribs, and the lower part is cylindrical. The three feet are three-bladed and extend at the boundary of the upper and lower parts if the second segment; their lengths are approximately equal to those of the apical and ventral horns. Shell wall of the lower part of the second segment is very thin. Pores in the second segment are circular to subcircular and randomly arranged, and they are larger than those in the first segment. Distal end of the second segment is fully open, without teeth.

***Dimensions*** (in $\mu$m) : Measurements are based on 23 specimens. Length of apical horn is 32–40 (36), ventral horn is 27–52 (42). Inside width between both **AL** is 33–43 (38), depth between **AL** and **VL** is 26–32 (28). Height of first segment (not including apical and ventral horns) is 30–40 (35), total height of shell (not including feet, apical and ventral horns) is 47–103 (74).

***Remarks*** : This species is distinguished from *Pseudodictyophimus gracilipes* (BAILEY) and *P. tanythorax* FUNAKAWA by the smaller pores in shell and upwardly acute angle of ventral horn. It is distinguished from *Tripodocyrtis elegans* FUNAKAWA by the presence of **V, VL** and a long ventral horn.

***Etymology*** : The specific name means "fine mesh" in Latin.

***Occurrences*** : MW-125, -120 and -118. Few in abundance.

***Stratigraphic notes*** : Lower Miocene.

### *Pseudodictyophimus pyramidalis* FUNAKAWA, sp. nov.

Plate 7, figs. 2a-3c

***Type specimens*** : Holotype is OCU CR-0021; paratype is OCU CR-0022.

***Description*** : Shell is composed of two segments. First segment is spherical. Shell wall of the first segment is very thick and its external surface is spineless. Apical rib is not recognized externally because it is completely buried in the thickened shell wall. Apical horn is three-bladed and its length is two to three times the height of the first segment. Ventral horn is three-bladed, shorter and thinner than the apical horn. Pores in the first segment are circular to subcircular and very small in diameter. In some specimens, pores are absent because of the thickened shell wall. The furrows between the two segments are distinct. In some specimens, there is one large pore on the apex of the first segment (Plate 7, fig. 3b). **A′** diverges from **A** at the junction of

**A** and **AL** (Plate 7, fig. 3c). Axial projection is distinct. In some specimens, there is one downward projection on the underside of both **L** (Plate 7, fig. 2b). Second segment is truncated conical, with three distinct dorsal and lateral ribs extending to three feet. Three feet are three-bladed and extend outside from the middle part of the second segment. They are shorter and narrower than the apical horn. Pores in the second segment are circular to subcircular and are not aligned; their diameter is larger than those in the first segment. Distal end of the second segment is fully open, with teeth.

***Dimensions*** (in $\mu$m) : Measurements are based on eight specimens. Length of apical horn is 65–88 (76), ventral horn is 22–27 (25). Outside diameter of first segment (not including apical and ventral horns) is 35–40 (38), second segment (not including feet) is 72–96 (86). Inside width between both **AL** is 36–40 (38) and depth between **AL** and **VL** is 32–35 (33). Height of first segment (not including apical horn) is 42–46 (44), total height of shell (not including feet and apical horn) is 87–104 (92).

***Remarks*** : This species is distinguished from *Pseudodictyophimus tanythorax* FUNAKAWA and *P. gracilipes* (BAILEY) by the truncated conical second segment and well-thickened shell wall of the first segment. It is distinguished from *P. leptoretis* FUNAKAWA by a very stout apical horn and thickened shell wall.

***Etymology*** : The specific name means "pyramidal" in Latin.

***Occurrences*** : MW-125 and -118. Rare to few in abundance.

***Stratigraphic notes*** : Lower Miocene.

### ***Pseudodictyophimus sphaerothorax*** **FUNAKAWA, sp. nov.**

Plate 8, figs. 1–3b

***Type specimen*** : Holotype is OCU CR-0023.

***Description*** : Shell is composed of two segments. The surface of the shell is smooth, without spines. First segment is subspherical. Apical rib is indistinct because it is buried in the thickened shell wall. Apical horn is three-bladed and longer than the height of the first segment. Ventral horn is three-bladed and shorter than the apical horn. Pores in the first segment are circular and are not aligned. In some specimens, the furrows between the first and second segments are indistinct because the shell wall is too thick to recognize furrows. **A′** diverges from **A** at the junction of **A** and **AL** (Plate 8, fig. 3b) and is hardly distinguished from other pore bars. Axial projection is distinct. **D** has no projection. There is one downward projection on the underside of both **L** (Plate 8, fig. 3b). Second segment is bell-shaped to hemispherical. Dorsal and lateral ribs are not recognized externally because they are buried in the thickened shell wall. Three feet are three-bladed and extend laterally and then curve downward. Their lengths are approximately equal to the height of the second segment. Pores in the second segment are circular, not aligned and larger than those in the first segment. Distal end of the second segment is round or is closed by a porous plate. Pores in the porous plate are irregularly shaped and not aligned.

***Dimensions*** (in $\mu$m) : Measurements are based on 49 specimens. Length of apical horn is 17–55 (37), ventral horn is 14–31 (23). Outside diameter of first segment (not including apical and ventral horns) is 28–48 (36), second segment (not including feet) is 45–110 (75), Inside width between both **AL** is 32–39 (35) and depth between **AL** and **VL** is 28–37 (31). Height of first segment (not including apical horn) is 19–43 (29), total height of shell (not including feet and apical horn) is 40–120 (78).

***Remarks*** : This species is distinguished from *Pseudodictyophimus leptoretis* FUNAKAWA by thickened shell and the fewer pores in shell. It is distinguished from *P. tanythorax* FUNAKAWA, *P. gracilipes* (BAILEY) and *P. pyramidalis* FUNAKAWA by rounded distal end of the second segment.

***Etymology*** : The specific name means "spherical thorax" in Latin.

***Occurrences*** : 90081402, MW-125, -120 and -118. Rare from the former one and common to abundant from the latter three.

***Stratigraphic notes*** : Upper Oligocene to Lower Miocene. This species occurs abundantly from the Lower Miocene.

### *Pseudodictyophimus tanythorax* FUNAKAWA

Plate 8, figs. 4–6

*Pseudodictyophimus tanythorax* FUNAKAWA, 1994, p. 473, Figures 12, 2a-3b.

***Remarks*** : Most Early Miocene specimens have thickened shell walls and very stout apical and ventral horns. Although they are distinguished from the Late Miocene form by the above-mentioned characters, both forms are placed in one species because the development of these characters are variable and change gradually. **A′** diverges from **A** at the junction of **A** and **AL** and is hardly recognized.

***Dimensions*** (in $\mu$m) : Measurements are based on 45 specimens. Length of apical horn is 38–68 (52), ventral horn is 15–32 (23). Outside diameter of first segment (not including apical and ventral horns) is 28–38 (33), second segment (not including feet) is 59–78 (69). Inside width between both **AL** is 26–33 (31) and depth between **AL** and **VL** is 27–33 (29). Height of first segment (not including apical horn) is 28–37 (32), total height of shell (not including feet, distal teeth and apical horn) is 65–105 (82).

***Occurrences*** : MW-125, -120 and -118. Few to common in abundance.

***Stratigraphic notes*** : First appearance of this species is within the Lower Miocene. Upper limit of this species is higher than the *Neodenticula kamtschatica* zone, Upper Miocene (FUNAKAWA, 1994).

### Genus *Steganocubus* SUGIYAMA, 1993

*Type species* : *Steganocubus subtilis* SUGIYAMA, 1993.

***Remarks*** : In this genus, two **L** are long and located inside the shell. First segment is distinguished from the second segment by the furrows along two **Al″** and two **V″l″** and these arches form an internal ring (**DR** in SUGIYAMA, 1993). It is obvious that the boundary of first and second segments is different from other Lophophaeninae. Two **AL** and two **VL** (or one **LL**) do not form the furrows in the shell wall because they are located inside the shell. Schematic diagrams of the internal skeletal structure of this genus are shown in Fig. 9.

SUGIYAMA (1993) defined the generic diagnosis of this genus as lacking **V**. In this study, species having **V** are included in this genus because of the similarities of most skeletal structures between them, except for having **V**. Furthermore comments are in the following specific remarks and in the last chapter of this paper.

### *Steganocubus incrassatus* FUNAKAWA, sp. nov.

Plate 9, figs. 1a-7

***Type specimens*** : Holotype is OCU CR-0024; paratypes are OCU CR-0025 to -0029.

***Description*** : Shell is composed of two segments. Internal skeletal structure is composed of **A, MB, D,** two **L, A′,** two **l′**, two **l″**, **V′**, **V″**, two **AL,** two **VL,** two **Al″** and two **V″l″**. **A** forms a short apical rib and a fine apical horn. **V′** and **V″** do not extend outside the shell. External surface of the shell is somewhat spiny, and in some specimens the surface is covered with a cobwebby meshwork layer (Plate 9, figs. 4a, 4b, 5a). First segment is hemispherical and in some specimens is irregularly shaped (Plate 9, figs. 3, 5a, 6b). Shell wall of the first segment is thickened and tends to be poreless in some specimens (Plate 9, fig. 2). Pores in the first segment, if they are present, are circular to subcircular and are not aligned. Their sizes are variable. Pore bars are very thick. In some specimens, pore bars are very rough, with large pores (Plate 9, fig. 3). Furrows along two **Al″** and two **V″l″** are indistinct in most specimens. Axial projection is distinct. A pair of trigonal to spiny projections (**l** ?)

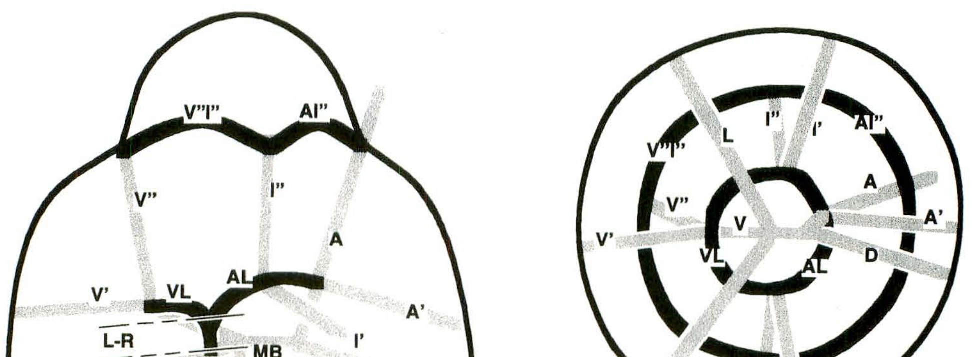



Fig. 9. Schematic diagrams of internal skeletal structure of *Steganocubus* : **1** is left lateral view; **2** is basal view. Gray elements are internal spicules and blacks are connecting arches. All abbreviations refer to the text.

are present on the lateral side of **D** (Plate 9, figs. 1b, 5b, 7), and in some specimens, these projections connect with the shell wall (Plate 9, figs. 5b, 7). On the lateral side of **L** there is a dorsally directed projection, and in some specimens this connects with the shell wall (Plate 9, fig. 7). Lateral and dorsal ribs and feet are not recognized. Second segment is cylindrical to bell-shaped. Pores in the second segment are circular to subcircular and are not aligned. Their sizes are variable. Pore bars are thick and some specimens have very rough pore bars with large pores (Plate 9, fig. 3). Distal end of the second segment is fully open, and in some specimens, it is closed by a cobwebby meshwork layer (Plate 9, fig. 4b).

***Dimensions*** (in $\mu$m) : Measurements are based on 25 specimens. Total height of shell is 66–104 (80), maximum diameter of shell is 69–91 (78). Width between both **AL** is 19–26 (22), depth between **LL** and the junction of **A** and **AL** is 18–25 (21).

***Remarks*** : This species is distinguished from *Steganocubus subtilis* SUGIYAMA by the roughly connected pore bars and the presence of an apical horn. This species has the large intraspecific variation of following structures : the development of the outer cobwebby meshwork layer, the thickness and roughness of the pore bars and the development of an apical horn. It is considered that this species is closely related to *S. subtilis* in evolutionary lineage because of the skeletal similarity.

***Etymology*** : The specific name means "thickened" in Latin.

***Occurrences*** : MW-125, -120 and -118. Few to common in abundance.

***Stratigraphic notes*** : Lower Miocene.

### ***Steganocubus irregularis*** FUNAKAWA, **sp. nov.**

Plate 10, figs. 1a-4

***Type specimens*** : Holotype is OCU CR-0030; paratypes are OCU CR-0031 and -0032.

***Description*** : Shell is composed of two segments. Internal skeletal structure is composed of **A, MB, D, V,** two **L, A′,** two **l′,** two **l″, V′, V″,** two **AL,** two **VL,** two **Al″** and two **V″l″**. External surface of the shell is somewhat spiny and in some specimens these spines diverge and connect with each other (Plate 10, fig. 2). First segment is irregularly shaped and is composed of roughly connected pore bars. In some specimens, **A** forms a short apical rib and a very fine apical horn (Plate 10, fig. 3a). Pores in the first segment are subcircular and are not aligned; their sizes are variable. Pore-bar arrangement in the first segment is random and very rough. In most specimens, **Al″** and **V″l″** are vague and some of them are absent. Furrows along them are indistinct. In some specimens, two **V′** are present (Plate 10, fig. 3b). Axial projection is distinct. In some specimens, **A′** is absent (Plate 10, fig. 3b). Second segment is irregularly cylindrical to bell-shaped. Lateral and dorsal ribs and feet are not recognized. Pores in the second segment are circular to subcircular and are not aligned; their sizes are variable. Pore bars in the second segment are very thick. Distal end of the second segment is fully open.

***Dimensions*** (in $\mu$m) : Measurements are based on 22 specimens. Total height of shell is 64–101 (84), maximum diameter of shell is 66–112 (93). Width between both **AL** is 21–29 (25), depth between the junction of **V** and **VL** and the junction of **A** and **AL** is 22–29 (24).

***Remarks*** : This species is characterized by the presence of **V** and two **VL** instead of one **LL.** It is distinguished from *S. subtilis* SUGIYAMA, *S. lipus* SUGIYAMA and *S. incrassatus* FUNAKAWA by the above-mentioned characters and the irregularly shaped shell.

Although the generic conception of *Steganocubus* is that it lacks **V**, the present species has stable **V.** This species has approximately equal internal and external skeletal structures to other *Steganocubus*, except for having **V.** The present author explains the presence of **V** as the intrageneric variation of this genus and places this species in *Steganocubus*.

***Etymology*** : The specific name means "irregular" in Latin.

***Occurrences*** : 90081306 and 90081402. Few to common in abundance.

***Stratigraphic notes*** : Upper Oligocene.

### Genus *Tripodocyrtis* FUNAKAWA, 1994

*Type species* : *Tripodocyrtis elegans* FUNAKAWA, 1994.

***Remarks*** : **A** forms an apical rib in the shell wall and an apical horn outside the shell. Connecting arches on the ventral side and **V** are absent. **D** and two **L** are well developed and form lateral and dorsal ribs in the shell wall of the second segment and three feet outside the shell. **A′** is poorly developed and is hardly recognized. Schematic diagrams of the internal skeletal structure of this genus are shown in Fig. 10.

### *Tripodocyrtis umbellaris* FUNAKAWA, sp. nov.

Plate 10, figs. 3a-4b

***Type specimens*** : Holotype is OCU CR-0033; paratype is OCU CR-0034.

***Description*** : Shell is composed of two segments. Internal skeletal structure is composed of **MB, A, D,** two **L** and two **AL.** External surface of the shell has numerous fine spines. First segment is hemispherical to cup-shaped, with a long apical horn. Apical horn is not bladed and its length is two to three times the height of the first segment. Pores in the first segment are subcircular and not aligned; their sizes are approximately same. The furrows between the first and second segments are restricted to the dorsal to lateral side of the shell and are shallow. **A′** diverges from **A** at the lower horizon than the junction of **A** and **AL** (Plate 10, fig. 6b). Axial projection is distinct. There are several projections on the underside to lateral side of both **L** and **D** (Plate 10, figs. 5b, 6b). Second segment is broadly expanded with distinct lateral and dorsal ribs. Three feet are variable in length, are not bladed and extend obliquely downward. Pores in the second segment are circular to subcircular, are not aligned and are larger than those in the first segment. Distal end of the second segment

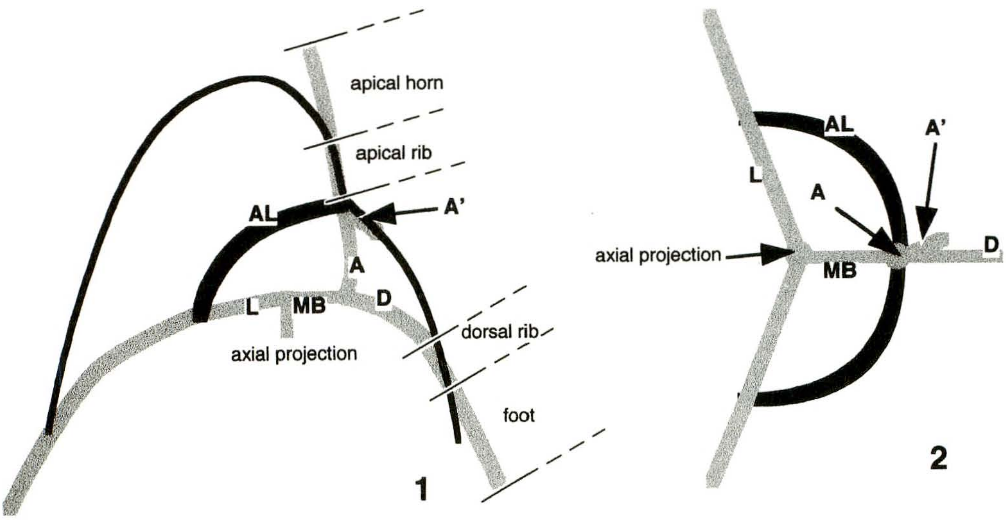



Fig. 10. Schematic diagrams of internal skeletal structure of *Tripodocyrtis umbellaris* FUNAKAWA, sp. nov. : **1** is left lateral view; **2** is basal view. Gray elements are internal spicules and black elements are connecting arches. All abbreviations refer to the text.

is fully open, without teeth.

***Dimensions*** (in $\mu$m) : Measurements are based on 14 specimens. Length of apical horn is 43–72 (57). Inside width of first segment between both **AL** is 33–43 (39), second segment (not including feet) is 83–164 (125). Total height of shell (not including feet and apical horn) is 47–86 (61).

***Remarks*** : This species has an almost similar skeleton to *T. elegans* FUNAKAWA, which occurs in the Upper Miocene, and is distinguished by a stout apical horn and the larger second segment. From other genera of Lophophaeninae, this species is distinguished by the absence of **V** and connecting arches on the ventral side of shell.

***Etymology*** : The specific name means "umbrella-shaped"in Latin.

***Occurrences*** : MW-125, -120 and -118. Rare to few in abundance.

***Stratigraphic notes*** : Lower Miocene.

## Intrageneric variation of internal skeletal structure

Intraspecific variation of internal skeletal structure was reported in some Late Miocene plagiacanthids (FUNAKAWA, 1994). In this study, intrageneric variations of internal skeletal structure are recognized in several genera of Late Oligocene to recent Lophophaeninae. Intrageneric variation of internal skeletal structure is defined as the different structures among species belonging to the same genus. In order to clear the intrageneric variation, the present author investigates internal skeletal structures of the following six genera of Lophophaeninae : *Peridium*, *Pseudocubus*, *Steganocubus*, *Pseudodictyophimus*, *Ceratocyrtis* and *Tripodocyrtis*.

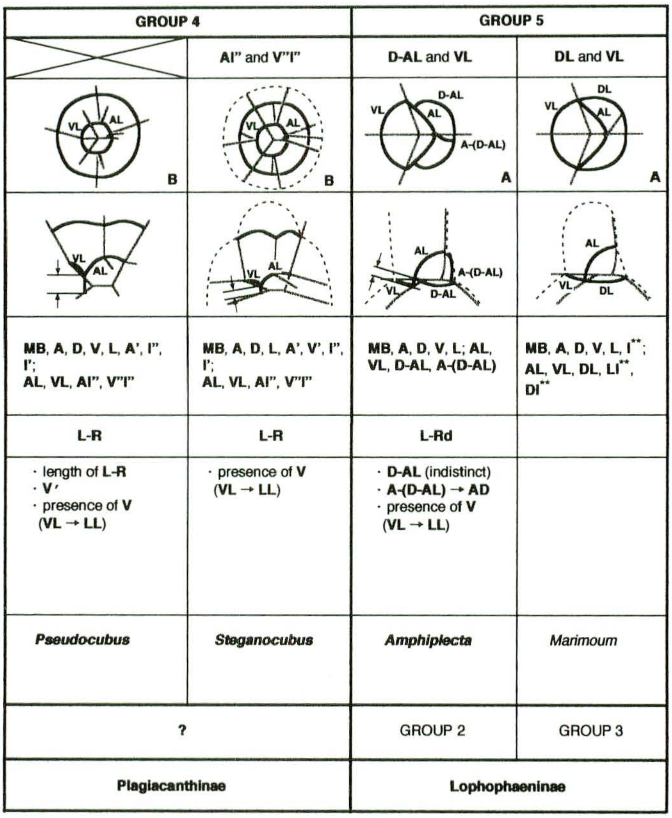



Fig. 11. Five groups of Lophophaeninae based on internal skeletal structure. Figures of *Peridium* are for *P. infundibuliforme* sp. nov.; *Pseudocubus* are for *P. praeobeliscus* sp. nov.; *Steganocubus* are for *S. incrassatus* sp. nov.; *Amphiplecta* are for *A. tripleura* sp. nov.; *Marimoum* are for the holotype specimen of *M. robustum* FUNAKAWA. Black solid lines are connecting arches; gray solid lines are internal spicules; black dotted lines are outlines of shell wall; * in composition of internal skeletal structure indicate an indistinct element, ** indicate an element which shows the intraspecific variation.

*Peridium* was defined in HAECKEL (1881). FUNAKAWA (1994) reported Late Miocene species, *P.* sp. aff. *P. spinipes* with its fine skeletal description. This species and the Early Miocene species, *P. infundibuliforme* FUNAKAWA, have a long interval of **A** between the junction to **MB** and that to **AL,** and in these species, **V** forms a ventral horn and does not form a ventral rib. On the other hand, the Late Oligocene species, *P. sphaerum* FUNAKAWA, has very short interval of **A** between the junction of **A** and **MB** and that of **A** and **AL. V** forms a ventral rib and does not form a ventral horn (Fig. 8). These skeletal characters are unchangeable at specific level and it is obvious that these skeletal differences on **A** and **V** represent the intrageneric variation in this genus.

*Pseudocubus* was defined in HAECKEL (1887) and included in Lophophaeninae by

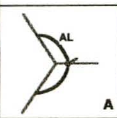
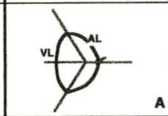
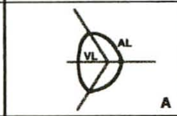
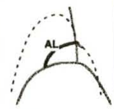
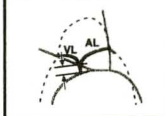
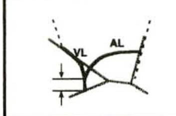
| | GROUP 1 | GROUP 2 | GROUP 3 |
|---|---|---|---|
| Arches subdividing two segments | only **AL** | **AL** and **VL** | **AL** and **VL** |
| Apical (**A**) or Basal (**B**) view |  |  |  |
| Left lateral view |  |  |  |
| Composition of internal skeletal structure | **MB, A, D, L, A'$^*$; AL** | **MB, A, D, V, L, A'$^*$; AL, VL** | **MB, A, D, V, L, A'; AL, VL** |
| Presence of **L-R** and **L-Rd** | | **L-R** | **L-R** |
| Intrageneric variation in internal skeletal structure | | · presence of **V** (**VL** → **LL**) | · length of **L-R**<br>· length of lower part of **A** between the junction of **A** and **AL** and that of **A** and **MB**<br>· presence of **A'**<br>· presence of **V** (**VL** → **LL**) |
| Generic composition (FUNAKAWA, 1994; **this paper**) | ***Tripodocyrtis*** | ***Ceratocyrtis***<br>*Lophophaena*<br>***Pseudodictyophimus*** | ***Peridium*** |
| FUNAKAWA (1994) | GROUP 1 | GROUP 2 | |
| PETRUSHEVSKAYA (1971b) | **Lophophaeninae** | | |

Fig. 11 continued

SUGIYAMA (1993). *P. obeliscus* HAECKEL is very abundant in plankton samples collected at Leg 1, St. 10 (Fig. 4), and has very short **L-R** that is hardly to be recognized. In addition, this species has long distinct **A'** and **V'**. PETRUSHEVSKAYA (1971b) reported this species from plankton samples collected in the Indian and Pacific Oceans and these specimens have solid **V**. Because PETRUSHEVSKAYA's sketches have also **A'**, **V'** and unrecognizable **L-R,** it is considered that the absence of **V** is an intraspecific variation of this species. On the other hand, *P. praeobeliscus* FUNAKAWA has distinct **L-R** and solid **V** without **V'**. The different lengths of **L-R** and the presence of **V'** between *P. obeliscus* and *P. praeobeliscus* represent the intrageneric variations in this genus (Fig. 9).

*Steganocubus* was defined in SUGIYAMA (1993) with the description of fine skeletal structures. Early to Middle Miocene species, *S. incrassatus* FUNAKAWA, *S. subtilis* SUGIYAMA and *S. lipus* SUGIYAMA lack **V**. The absence of **V** was one of the diagnostic characters of this genus in SUGIYAMA (1993). On the other hand, the Late Oligocene species, *S. irregularis* FUNAKAWA, has stable **V**. Because of the similarity of the skeletal structure among them, it is hardly possible to locate *S. irregularis* in other genus. Therefore, the absence of **V** is not the generic character but the intrageneric variation of this genus.

Many species of *Pseudodictyophimus* from various ages in Cenozoic time have been reported up to the present. Their fine skeletal structures were described by some authors; *P. gracilipes* (BAILEY) was described by PETRUSHEVSKAYA (1971b) from plankton samples and FUNAKAWA (1994) from the Upper Miocene, *P. tanythorax* FUNAKAWA was by FUNAKAWA (1994) from the Upper Miocene. In this paper, *P. gracilipes*, *P. tanythorax*, *P. leptoretis* FUNAKAWA, *P. sphaerothorax* FUNAKAWA and *P. pyramidalis* FUNAKAWA are described from the Upper Oligocene to the Lower Miocene. All these examined species have the same internal skeletal structure, and intrageneric variation among them is not recognized.

Several species of *Ceratocyrtis* from various ages have been reported with the information on their internal skeletal structures; *C. histricosus* (JØRGENSEN) was described by PETRUSHEVSKAYA (1971b) from plankton samples, and by FUNAKAWA (1994) from the Upper Miocene, *C. multicornus* FUNAKAWA by FUNAKAWA (1994) from the Upper Miocene. *C. morawanensis* FUNAKAWA from the Upper Oligocene is described in this paper. These species have similar internal skeletal structures, and intrageneric variation is not recognized among them.

*Tripodocyrtis* was defined in FUNAKAWA (1994). *T. elegans* FUNAKAWA was described by FUNAKAWA (1994) from the Upper Miocene with its internal skeletal structure. The present author describes *T. umbellaris* FUNAKAWA from the Lower Miocene and shows its fine skeletal structure. Between these two species there is no difference in internal skeletal structure.

## Classificatory significance of intrageneric variation in internal skeletal structure

Lophophaeninae was emended in PETRUSHEVSKAYA (1971a) as one subfamily of Plagiacanthidae (PETRUSHEVSKAYA 1971a, p. 989). FUNAKAWA (1994) examined Late Miocene Lophophaeninae and indicated that this subfamily may be polyphyletic and distinguished three groups that have similar internal skeletal structures (FUNAKAWA, 1994, fig. 16). In this paper, five groups are recognized in Late Oligocene to Late Miocene Lophophaeninae. Although some groups from the Upper Miocene have similar internal skeletal structures, they are distinguished by the patterns of their intrageneric variation in the internal skeletal structure.

1) GROUP 1 is represented by *Tripodocyrtis*. Two species of this genus have similar internal skeletal structures and do not show the intrageneric variation in internal skeletal structure. Other genera that do not have **V** and ventral side connecting arches are not known till now. To clarify the phylogeny of this group, it is necessary to examine the pre-Miocene species of this group. This group is equal to "GROUP 1" of FUNAKAWA (1994).

2) GROUP 2 is composed of *Ceratocyrtis*, *Lophophaena* and *Pseudodictyophimus*. The

intrageneric variation in internal skeletal structure is not recognized in all examined species of these three genera in FUNAKAWA (1994) and this paper. This group corresponds to parts of "GROUP 2" of FUNAKAWA (1994).

3) GROUP 3 is represented by *Peridium*. Although Miocene species of this genus have similar internal skeletal structures to that of GROUP 2 *Ceratocyrtis*, *Lophophaena* and *Pseudodictyophimus*, Late Oligocene species of this genus have different internal skeletal structures to those of *Ceratocyrtis*, *Lophophaena* and *Pseudodictyophimus*. It is possible that the similarity of internal skeletal structure between GROUP 2 and GROUP 3 in Late Miocene time indicates the result of convergence in each group. Further study is needed to clear the generic phylogeny and the process of convergence in internal skeletal structure in these GROUPS. This group includes *Cryptogyrus* SUGIYAMA, 1993 and, perhaps, some of Lophophaeninae, for example, *Arachnocorallium* HAECKEL, 1887 emend. PETRUSHEVSKAYA, 1971b, *Dimelissa* CAMPBELL, 1951 emend. PETRUSHEVSKAYA, 1971b, *Peromelissa* HAECKEL, 1881 emend. PETRUSHEVSKAYA, 1971b and *Psilomelissa* HAECKEL, 1881. This group corresponds to parts of "GROUP 2" of FUNAKAWA (1994).

4) GROUP 4 is composed of *Pseudocubus* and *Steganocubus*. All known species of these genera have four props (two **l″**, **V″** and **A**) and four arches connecting these props (two **Al″** and two **V″l″**) and these internal skeletal structures are absent in other Lophophaeninae.

5) GROUP 5 is composed of *Amphiplecta* and *Marimoum*. These two genera have similar internal skeletal structures although the former genus presents the intrageneric variation with the presence of **D-AL**. Because these arches are never recognized in GROUPS 1, 2, 3 and 4, this group forms a different phylogeny.

To establish the suprageneric classification of Lophophaeninae, it is necessary to consider the intrageneric variation in internal skeletal structure through intrageneric lineage, because there are the possibilities of convergence in internal skeletal structure such as that between GROUPS 2 and 3.

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**Plate 1**

Figures **1a-3b** : *Amphiplecta tripleura* FUNAKAWA, sp. nov.

**1a-1c** : OCU CR-0007, MW-125, holotype.

**1a** : right lateral view, ×375; arrow 1 points to **A** which forms a long apical rib, 2 to **V** which forms a fine ventral horn. **1b** : basal view, ×750; white arrow points to **A-[D-AL]**. **1c** : enlargement from dorsal to right lateral side for internal skeletal structure, ×1000; white arrows point to downward projections on the underside of **L**, black arrows to lateral projections on **A**.

**2** : MW-125, apical view, ×375; white arrow points to a lateral projection (**l?**) on **D**.

**3a-3b** : MW-125.

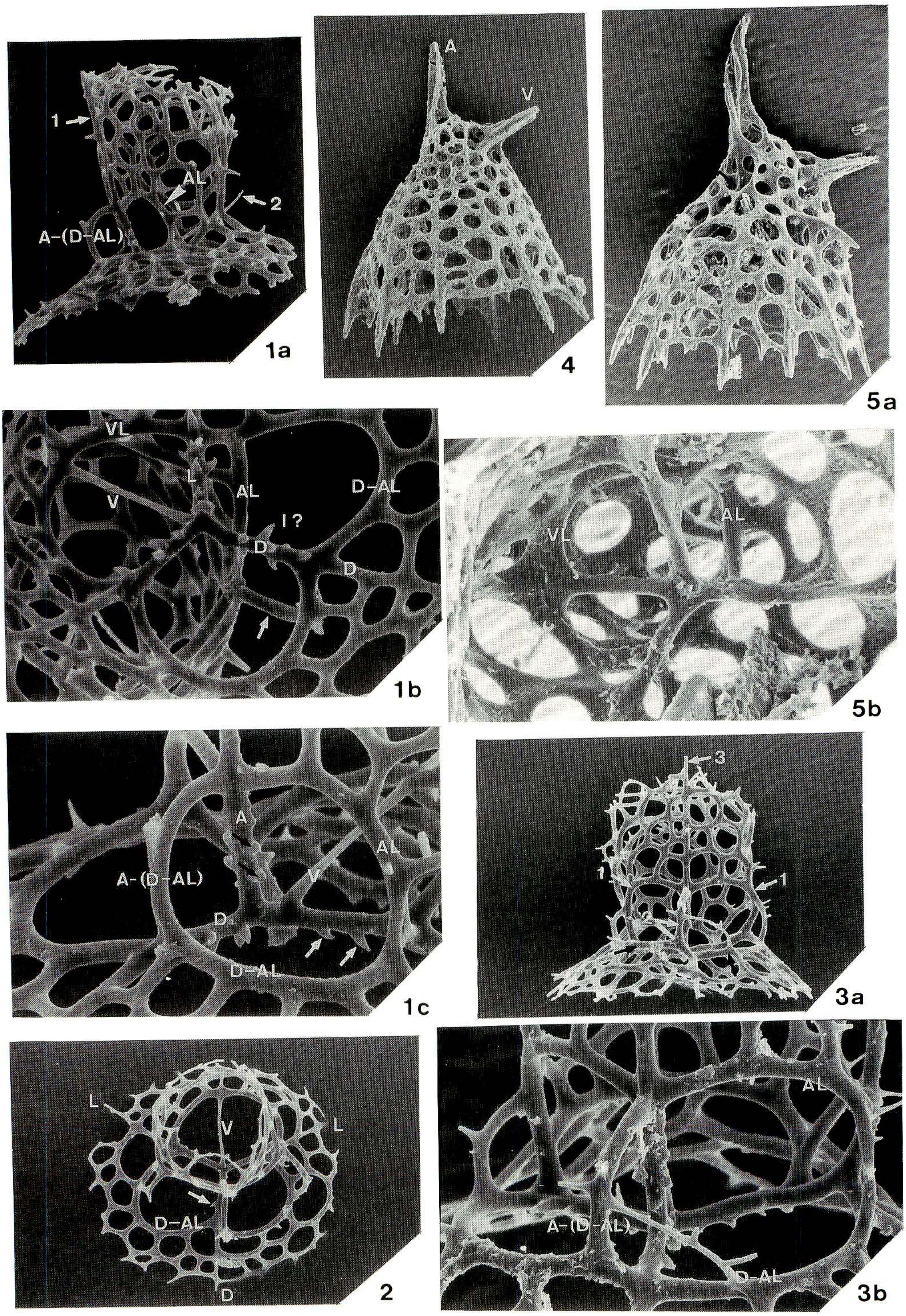
**3a** : dorsal view, ×375; arrows 1 point to **AL**, 2 to **A-(D-AL)**, 3 to **A** which forms a short apical horn. **3b** : enlargement from dorsal to right lateral side for internal skeletal structure, ×1000.

Figures **4–5b** : *Ceratocyrtis morawanensis* FUNAKAWA, sp. nov.

**4** : 90081302, right lateral view, ×250.

**5a-5b** : OCU CR-0008, 90081501, holotype.

**5a** : right lateral view, ×250; black arrow points to **A′**. **5b** : basal view, ×750.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A
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A-(D-AL)
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D-AL
1c
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1
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3a
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V
L
D-AL
D
2
AL
A-(D-AL)
D-AL
3b

**Plate 2**

Figure **1a–4b** : *Peridium sphaerum* FUNAKAWA, sp. nov.

**1a-1d** : OCU CR-0011, 90081501, holotype.

**1a** : right lateral view, ×500. **1b** : enlargement from left lateral side for internal skeletal structure, ×1750. **1c** : dorsal view, ×1000; white arrow points to **VL.** **1d** : basal view, ×1000; white arrow points to an axial projection.

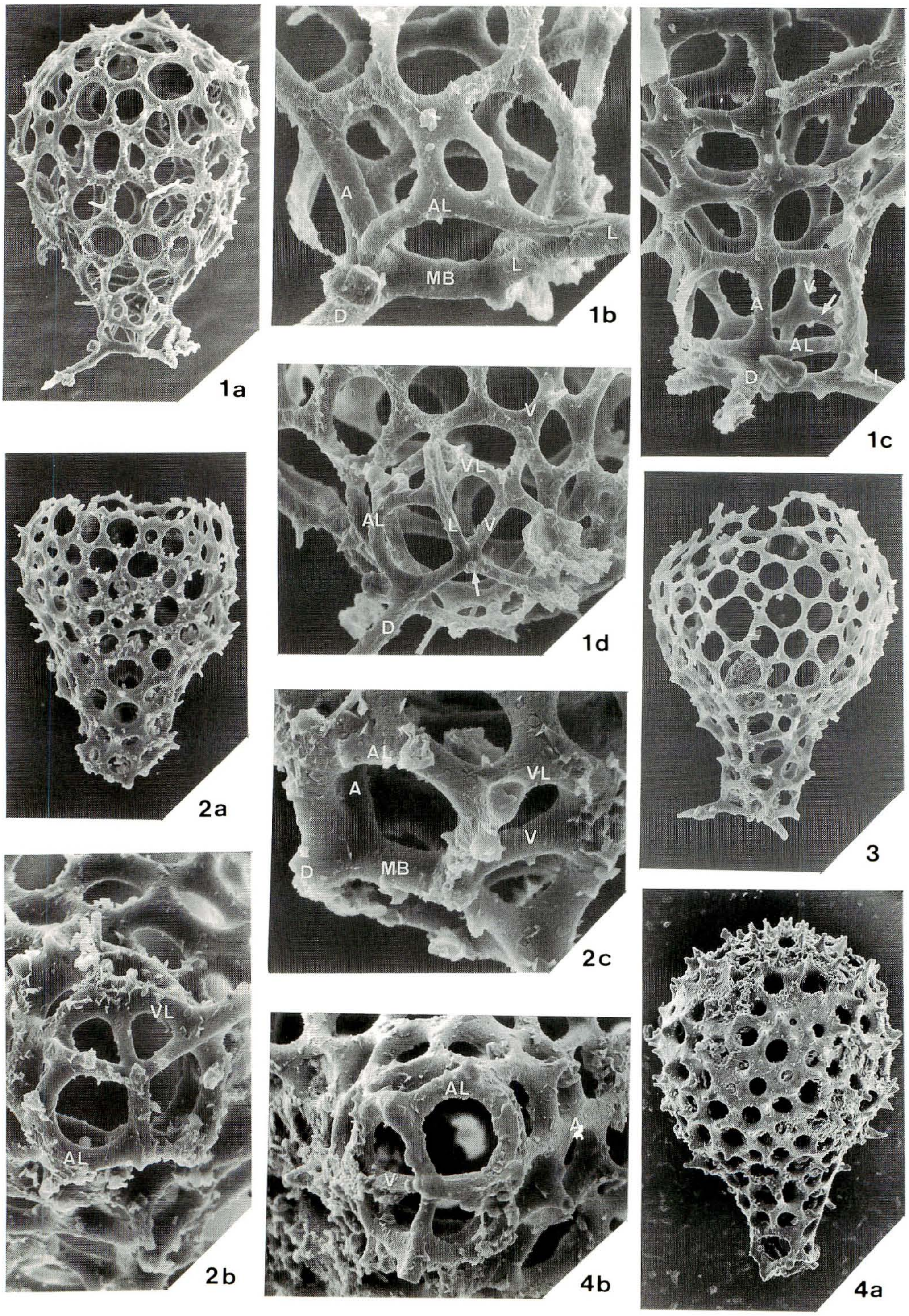
**2a-2c** : OCU CR-0012, 90081306, paratype.

**2a** : right lateral view, ×375. **2b** : basal view, ×1000. **2c** : right lateral view, ×1750.

**3** : 90081306, right lateral view, ×375.

**4a-4b** : OCU CR-0013, 90081306, paratype.

**4a** : left lateral view, ×375. **4b** : basal view, ×1000.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2b
AL
A
V
4b
4a

**Plate 3**

Figures **1a-4** : *Peridium infundibuliforme* FUNAKAWA, sp. nov.

**1a-1d** : OCU CR-0014, MW-125, holotype.

**1a** : left lateral view, × 500. **1b** : enlargement from left lateral side for internal skeletal structure, × 1000; white arrow points to a downward projection on the underside of **D.** **1c** : enlargement from basal side for internal skeletal structure, × 1000; arrow 1 points to a downward projection on the underside of **D,** 2 to a pair of lateral projections (**l** ?) on **D,** 3 to an axial projection. **1d** : enlargement from ventral side for internal skeletal structure, × 1750.

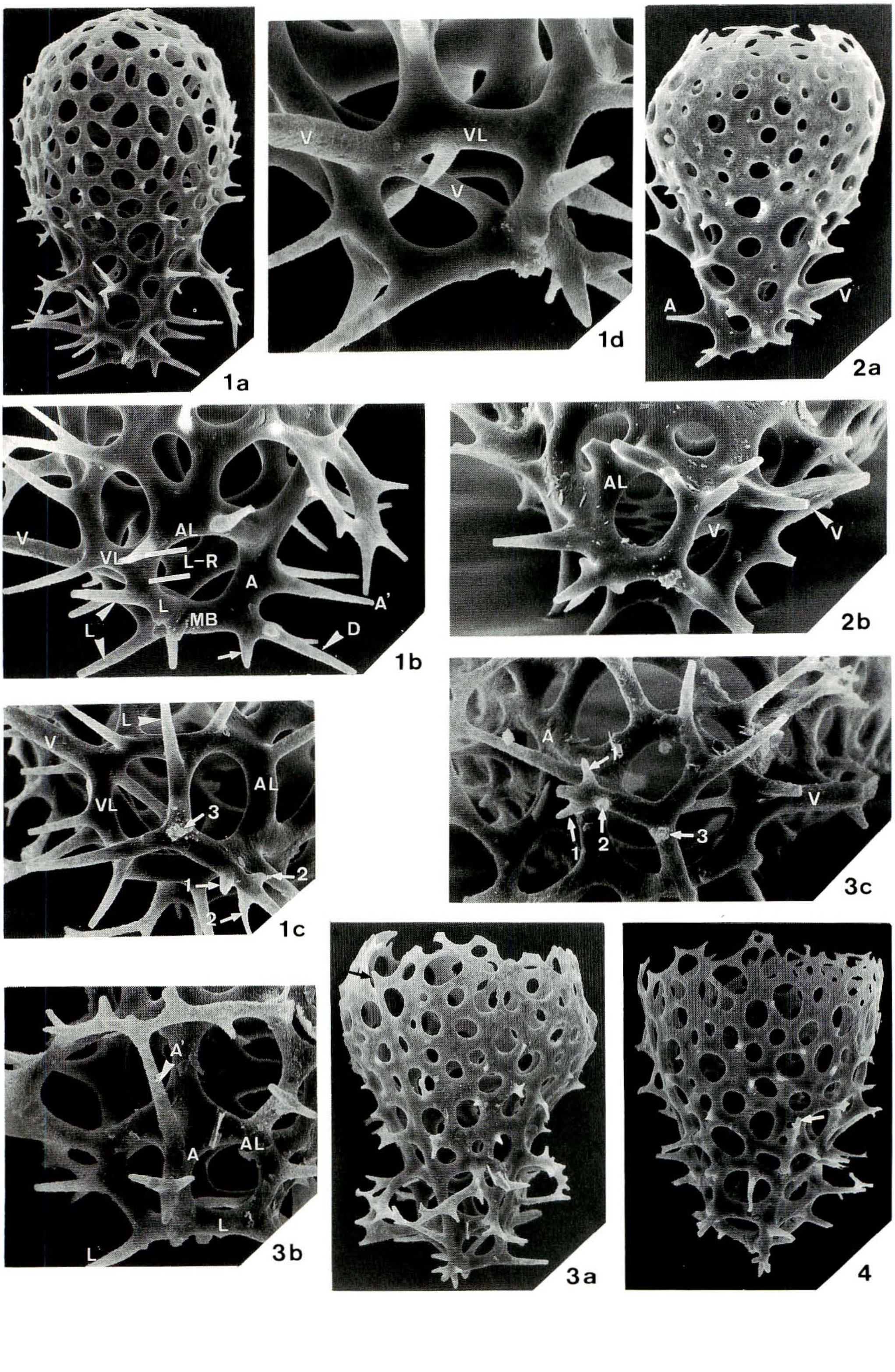
**2a-2b** : MW-125.

**2a** : right lateral view, × 500. **2b** : basal view, × 1000.

**3a-3c** : OCU CR-0015, MW-125, paratype.

**3a** : dorsal to right lateral view, × 500; black arrow points to **A** which forms a very fine apical horn. **3b** : enlargement from dorsal side for internal skeletal structure, × 1000. **3c** : enlargement from basal side for internal skeletal structure, × 1000; arrows 1 point to a pair of lateral projections (**l** ?) on **D,** 2 to a downward projection on the underside of **D,** 3 to an axial projection.

**4** : MW-125, dorsal view, × 500; white arrow points to **A** which forms a very fine apical horn.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## Plate 4

Figures **1a-1d** : *Pseudocubus praeobeliscus* FUNAKAWA, sp. nov., OCU CR-0016, MW-125, holotype.

**1a** : left lateral view, ×500. **1b** : enlargement from left lateral side for internal skeletal structure, ×1000. **1c** : enlargement from dorsal side for internal skeletal structure, ×1000; white arrow points to a lateral projection on **A.** **1d** : enlargement from obliquely basal side for internal skeletal structure, ×1000.

**2a-3b** : *Pseudocubus obeliscus* HAECKEL (Leg 1, St. 10, plankton samples).

**2a** : ventral view, ×375. **2b** : enlargement from ventral side for internal skeletal structure, ×1000; white arrows point to a pair of lateral projections (**1** ?) on **D.**

**3a** : ventral to left lateral view, ×375. **3b** : enlargement from ventral to left lateral side for internal skeletal structure, ×1000; arrows **1** point to a pair of lateral projections (**1** ?) on **D,** 2 to an axial projection.

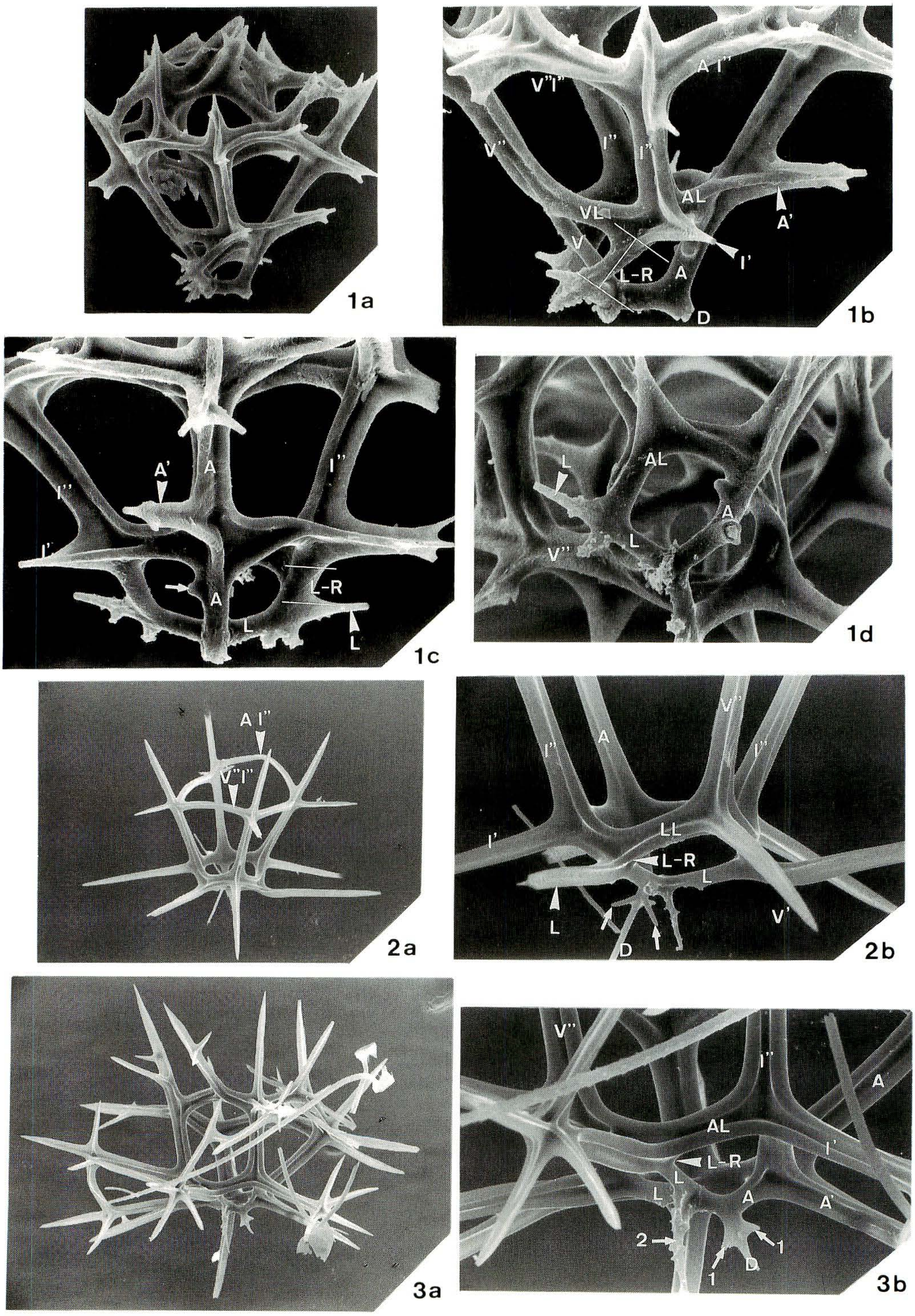

1a
V"I"
A I"
V"
I"
I"
AL
A'
VL
V
I'
L-R
A
D
1b
A'
A
I"
I"
I'
L-R
A
L
L
1c
L
AL
A
V"
L
1d
A I"
V"I"
2a
V"
I"
A
I"
LL
I'
L-R
L
L
D
V'
2b
3a
V"
I"
A
AL
L-R
I'
L
L
A
A'
2
1
1
D
3b

**Plate 5**

Figures **1a-3c** : *Pseudocubus praeobeliscus* FUNAKAWA, sp. nov.

**1a-1c** : OCU CR-0017, 90091607 (the Taiki Formation, Upper Miocene, eastern Hokkaido), paratype.

**1a** : right lateral view, ×375. **1b** : enlargement from right lateral side for internal skeletal structure, ×1750. **1c** : enlargement from dorsal side for internal skeletal structure, ×1000; white arrows point to downward projections on the underside of **L,** black arrows to a pair of lateral projections on **A.**

**2a-2b** : OCU CR-0018, MW-125, paratype.

**2a** : dorsal view, ×375; black arrows point to a pair of lateral projections on **A.** **2b** : apical view, ×500.

**3a-3c** : MW-125.

**3a** : right lateral view, ×500. **3b** : enlargement from obliquely basal side for internal skeletal structure, ×1000; white arrows point to a pair of lateral projections (**l** ?) on **D.** **3c** : enlargement from dorsal side for internal skeletal structure, ×1000; white arrows point to a pair of lateral projections on **A.**

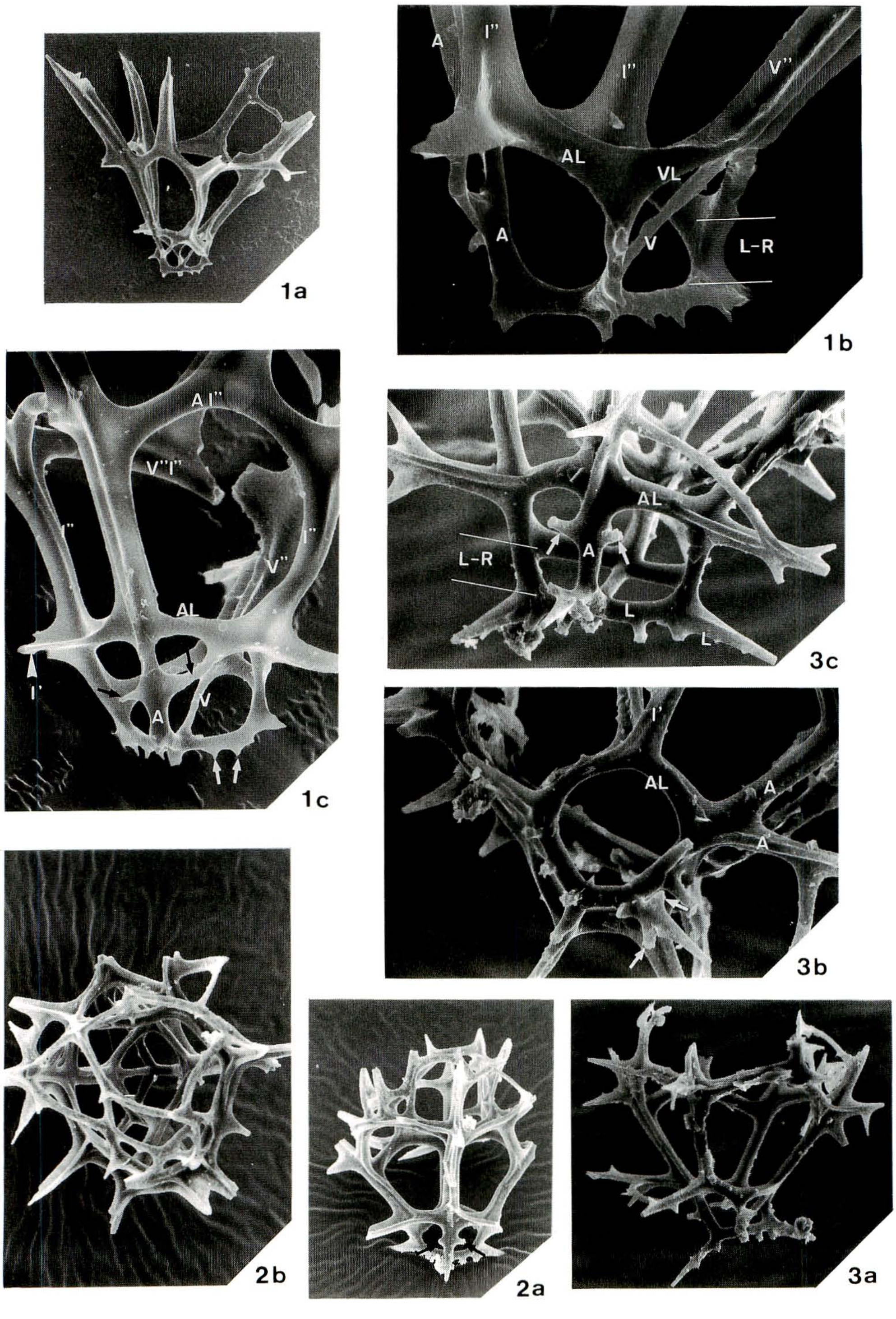

1a
A
I"
I"
V"
AL
VL
A
V
L-R
1b
AI"
V"I"
I"
I"
V"
AL
I'
A
V
1c
AL
L-R
A
L
L
3c
I'
AL
A
A
3b
2b
2a
3a

**Plate 6**

Figures **1–2c** : *Pseudodictyophimus gracilipes* (BAILEY)

**1** : MW-125, right lateral view, ×375.

**2a-2c** : 90081306.

**2a** : right lateral view, ×375. **2b** : basal view, ×1000. **2c** : enlargement from basal side for internal skeletal structure, ×1750.

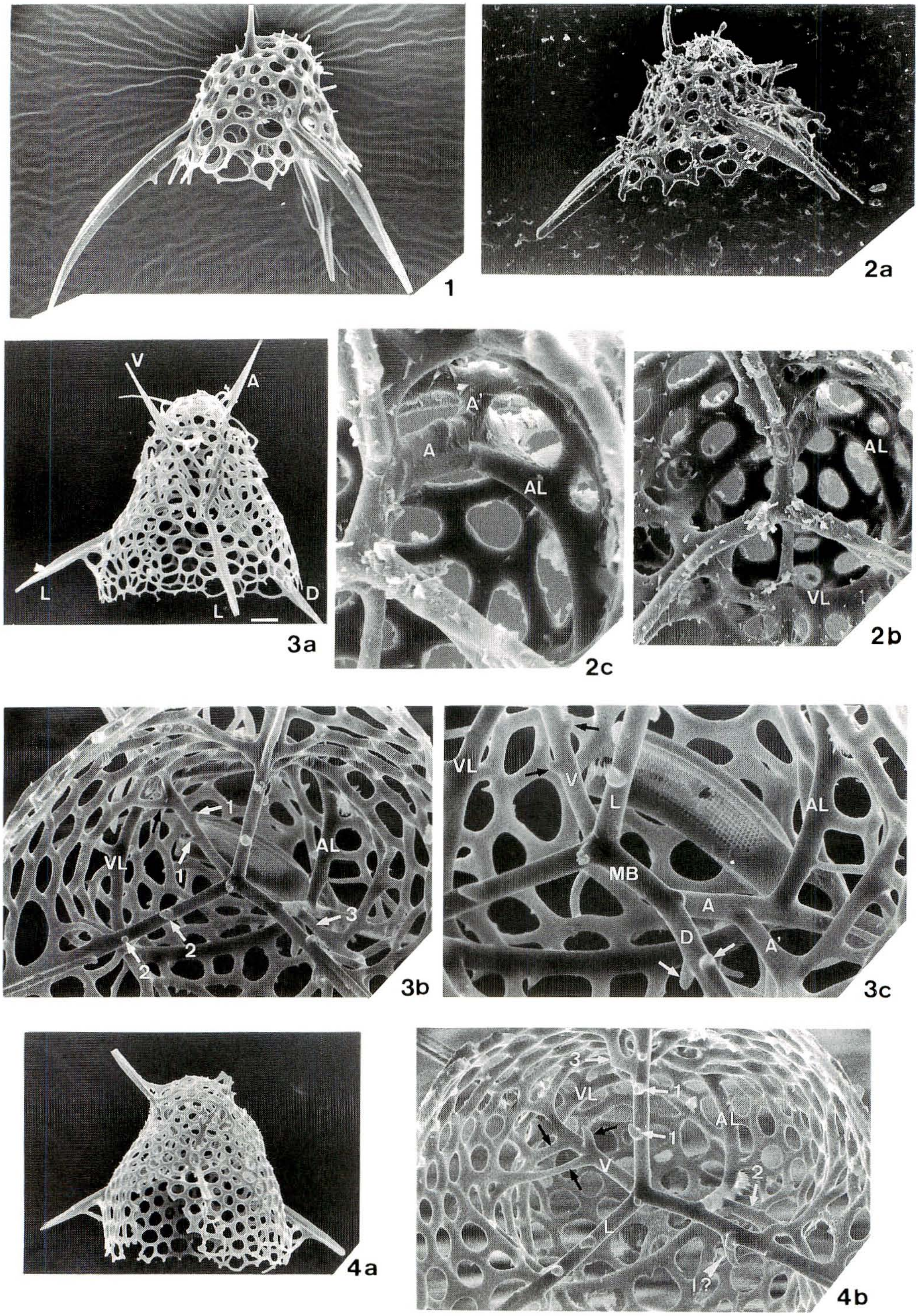
Figure **3a-4b** : *Pseudodictyophimus leptoretis* FUNAKAWA, sp. nov.

**3a-3c** : OCU CR-0019, MW-125, holotype.

**3a** : left lateral view, ×375. **3b** : basal view, ×1000; white arrows 1 point to projections on the lateral side of **V,** 2 to downward projections on the underside of **L,** 3 to **A′,** black arrow to a projection on the lateral side of **V** that connects to the shell wall. **3c** : enlargement from basal side for internal skeletal structure, ×1750; arrow 1 points to a lateral projection (**l** ?) on **D,** 2 to a downward projection on the underside of **D,** black arrows to lateral projections on **V.**

**4a-4b** : MW-125.

**4a** : left lateral view, ×375. **4b** : basal view, ×1000; arrows 1 point to downward projections on the underside of **L,** 2 to **A′,** 3 to a skeleton diverged from **L,** black arrows to lateral projections on **V** and some of them connect with shell wall.


1
2a
V
A
L
L
D
3a
A'
A
AL
2c
AL
VL
2b
1
VL
1
AL
3
2
2
3b
VL
V
L
AL
MB
A
D
A'
3c
4a
3
VL
1
AL
1
V
2
L
1?
4b

## Plate 7

Figures **1a-1c** : *Pseudodictyophimus leptoretis* FUNAKAWA, sp. nov., OCU CR-0020, MW-125, paratype.

**1a** : right lateral view, ×375. **1b** : basal view, ×750; white arrows point to downward projections on the underside of **L.** **1c** : enlargement from basal side for internal skeletal structure, ×1750; white arrows point to lateral to downward projections on **V.**

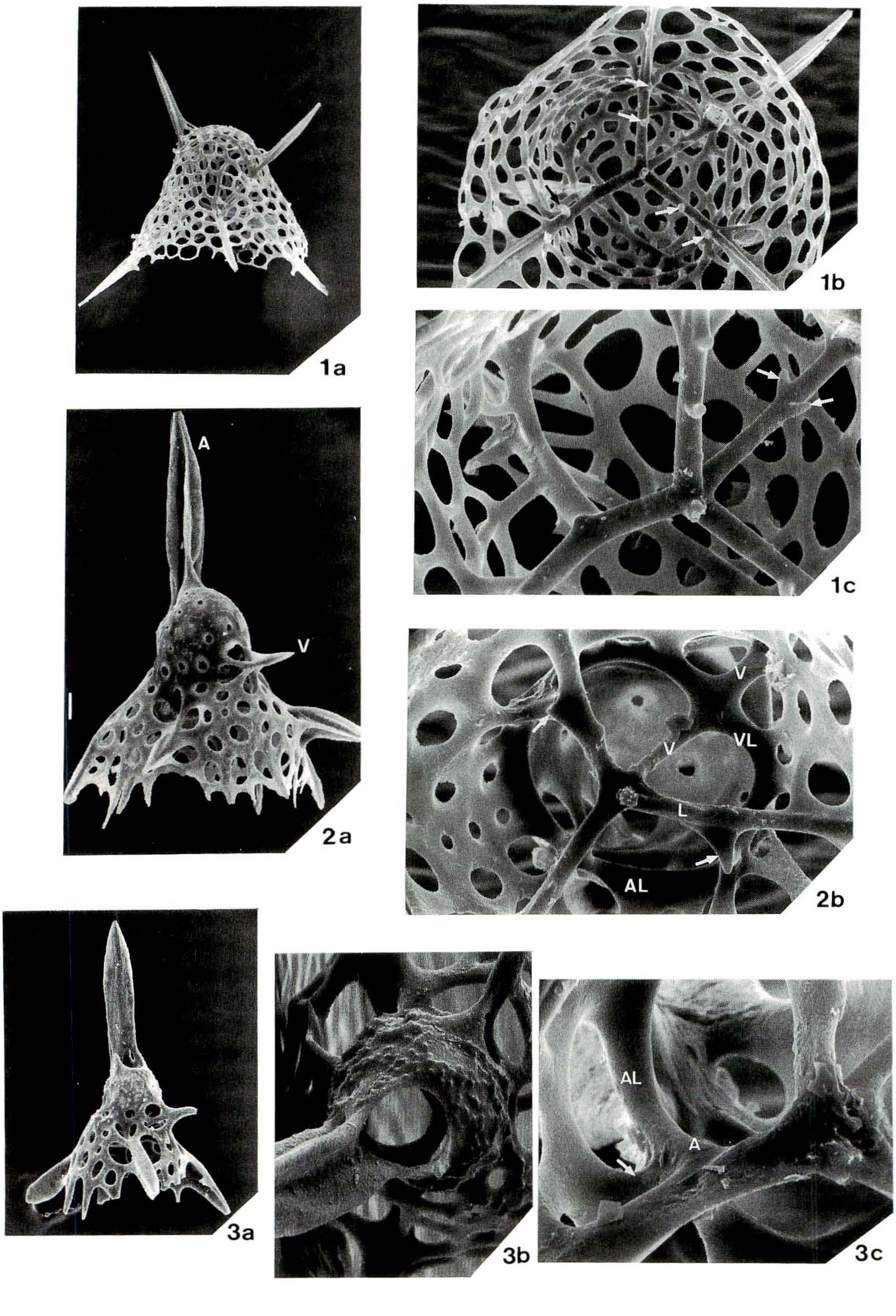
Figures. **2a-3c** : *Pseudodictyophimus pyramidalis* FUNAKAWA, sp. nov.

**2a-2b** : OCU CR-0021, MW-125, holotype.

**2a** : right lateral view, ×375. **2b** : enlargement from basal side for internal skeletal structure, ×1000; white arrows point to downward projections on **L.**

**3a-3c** : OCU CR-0022, MW-125, paratype.

**3a** : right lateral view, ×250. **3b** : apical view, ×750. **3c** : enlargement from basal side for internal skeletal structure, ×1750; white arrow points to **A′.**


1a
1b
1c
A
V
2a
V
V
VL
L
AL
2b
3a
3b
AL
A
3c

## Plate 8

Figures **1–3b** : *Pseudodictyophimus sphaerothorax* FUNAKAWA, sp. nov.

**1** : OCU CR-0023, MW-125, holotype, left lateral view, ×375.

**2a-2b** : MW-125.

**2a** : right lateral view, ×375. **2b** : obliquely basal view, ×500.

**3a-3b** : MW-118, broken specimen.

**3a** : right lateral view, ×375. **3b** : basal view, ×750; white arrows point to downward projections on the underside of **L,** black arrow to **A′**.

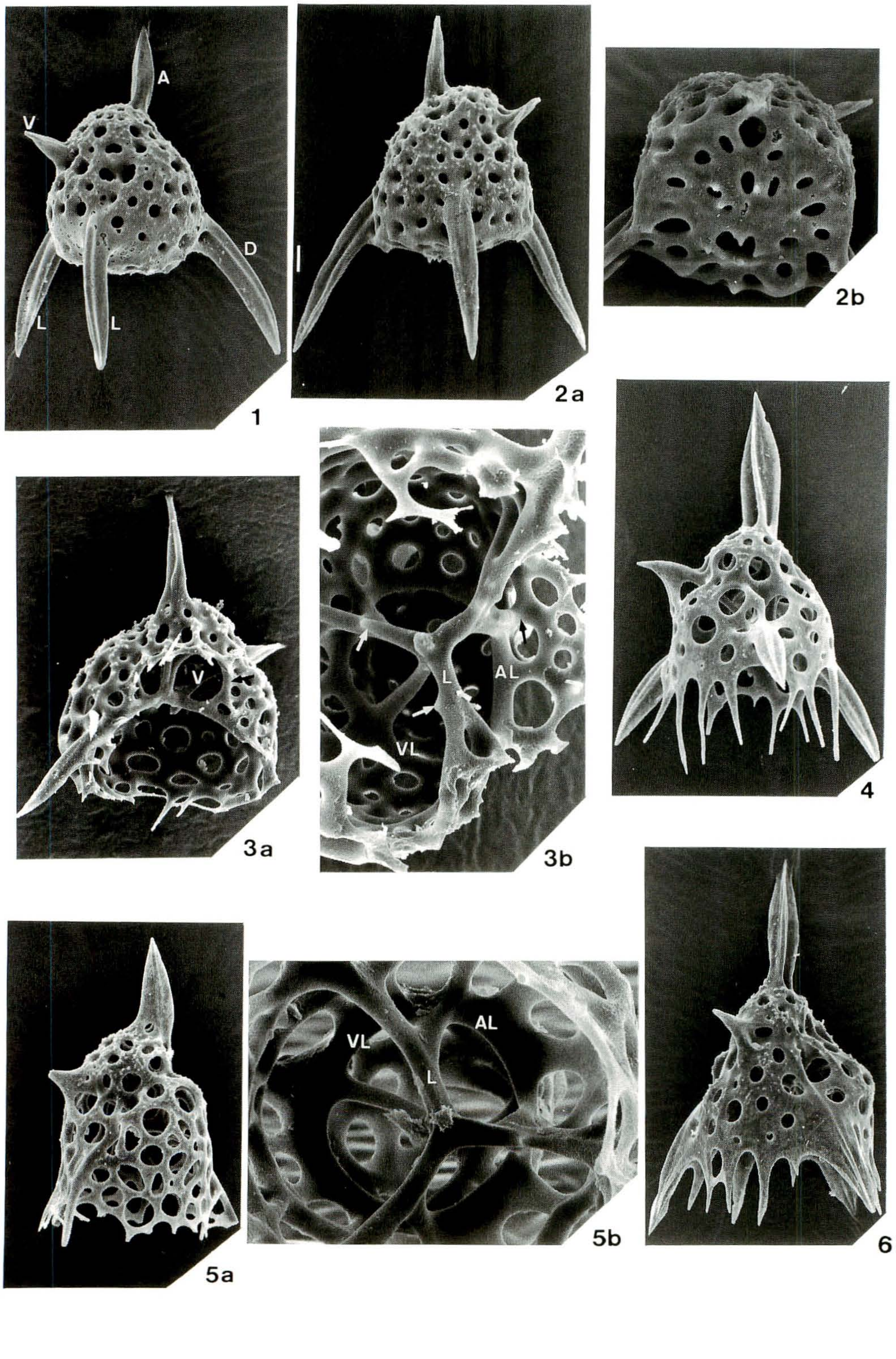
Figures. **4-6** : *Pseudodictyophimus tanythorax* FUNAKAWA

**4** : MW-125, left lateral view, ×375.

**5a-5b** : MW-125.

**5a** : left lateral view, ×375. **5b** : basal view, ×1000.

**61** : MW-125, ventral to left lateral view, ×375.


A
V
D
L
L
1
2a
2b
V
3a
AL
L
VL
3b
4
5a
VL
AL
L
5b
6

## Plate 9

Figures **1a-7** : *Steganocubus incrassatus* FUNAKAWA, sp. nov.

**1a-1c** : OCU CR-0024, MW-125, holotype.

**1a** : left lateral view, ×500. **1b** : basal view, ×750; arrow 1 points to **A,** 2 to **l″**, 3 to **V″**, 4 to **A′**, 5 to lateral projections (**1** ?) on **D**. **1c** : enlargement from basal side for internal skeletal structure, ×1750.

**2** : OCU CR-0025, MW-125, paratype, right lateral view, ×500.

**3** : OCU CR-0026, MW-125, paratype, right lateral view, ×500.

**4a-4b** : OCU CR-0027, MW-125, paratype.

**4a** : ventral view, ×375. **4b** : basal view, ×500.

**5a-5b** : OCU CR-0028, MW-125, paratype.

**5a** : dorsal view, ×500. **5b** : basal view, ×750; white arrows point to lateral projections (**1** ?) on **D,** one of them connects with shell wall.

**6** : OCU CR-0029, MW-125, paratype, right lateral view, ×500.

**7** : MW-125, basal view, ×750; arrows 1 point to lateral projections (**1** ?) on **D,** one of them connects with shell wall, 2 to a lateral projection on **L,** that connects with shell wall.

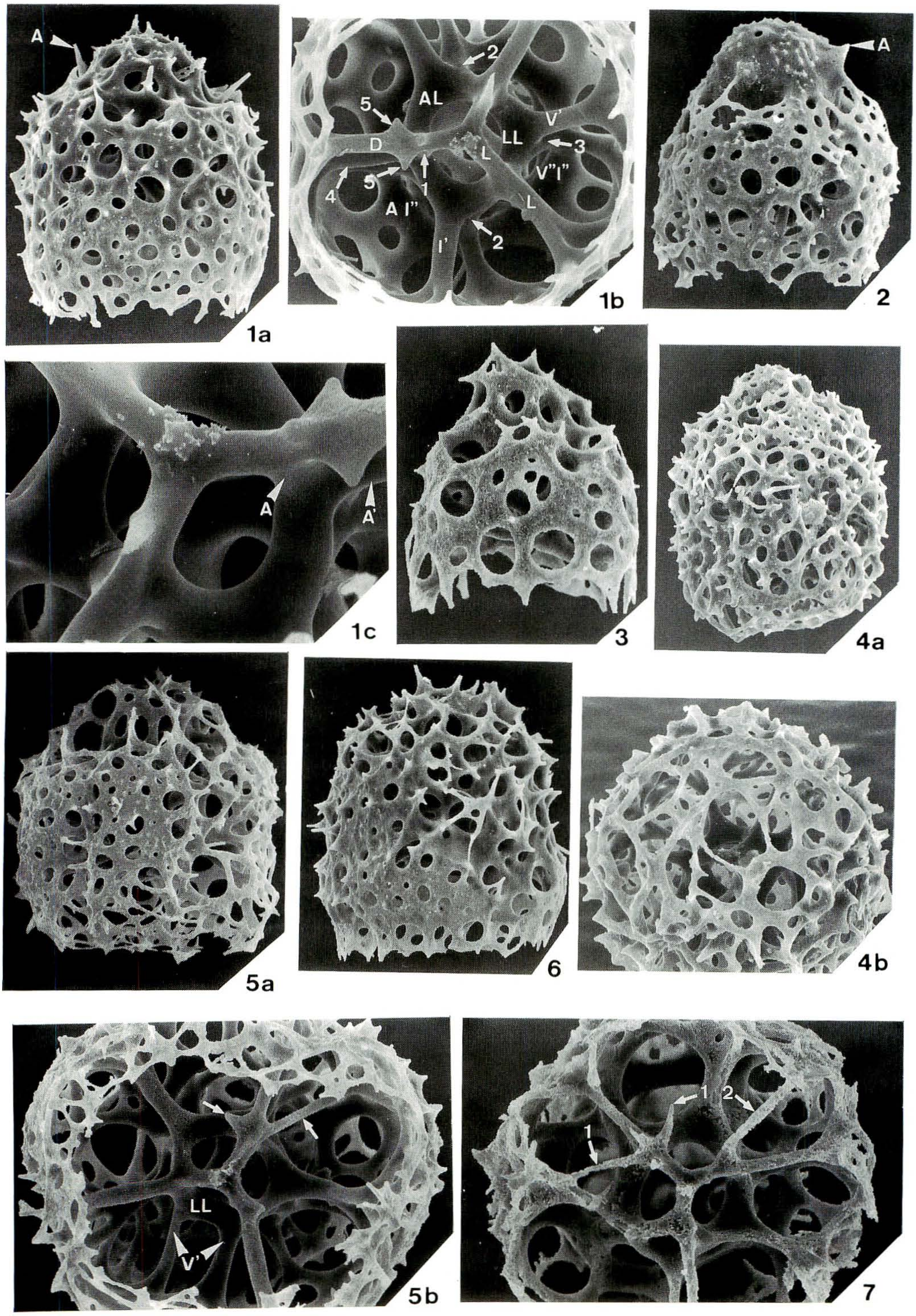

A
1a
2
AL
5
D
LL
V'
3
L
V"l"
4
5
1
A l"
l'
2
1b
A
2
A
A'
1c
3
4a
5a
6
4b
LL
V'
5b
1
2
1
7

**Plate 10**

Figures **1a-4** : *Steganocubus irregularis* FUNAKAWA, sp. nov.

**1a-1b** : OCU CR-30, 90081402, holotype.

**1a** : left lateral view, ×375. **1b** : basal view, ×750.

2 : 90081402, ventral view, ×375.

**3a-3b** : OCU CR-0031, 90081306, paratype.

**3a** : right lateral view, ×375; white arrow points to **A** which forms a fine apical horn. **3b**: enlargement from basal side for internal skeletal structure, ×1000.

**4** : OCU CR-0032, 90081306, paratype, ventral view, ×500.

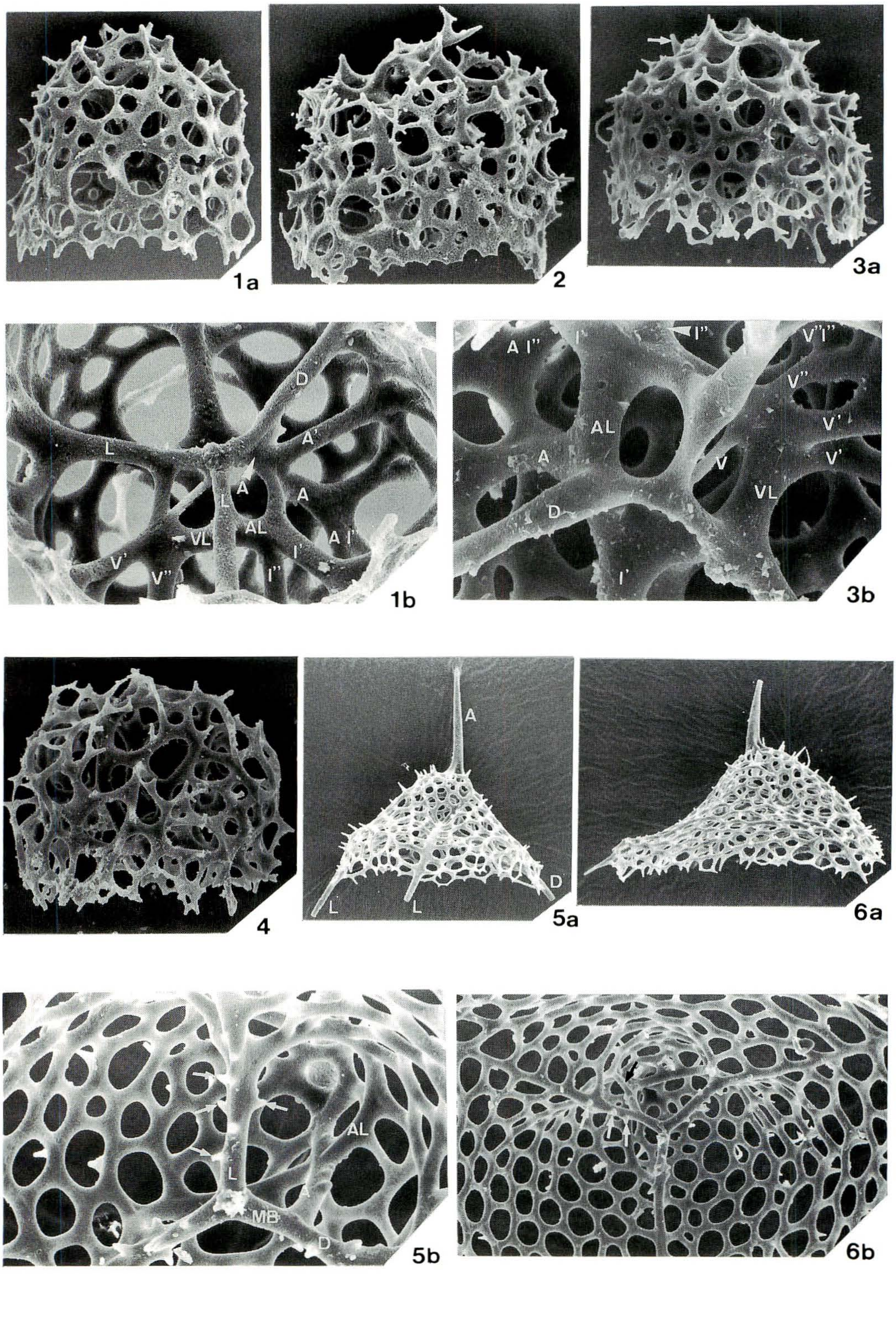
Figures **5a-6b** : *Tripodocyrtis umbellaris* FUNAKAWA, sp. nov.

**5a-5b** : OCU CR-0033, MW-125, holotype.

**5a** : left lateral view, ×250. **5b** : enlargement from basal view for internal skeletal structure, ×1000; white arrows point to lateral to downward projections on **L.**

**6a-6b** : OCU CR-0034, MW-125, paratype.

**6a** : right lateral view, ×250. **6b** : basal view, ×500; white arrows point to downward projections on **D,** black arrow to **A′**.


1a
2
3a
D
L
A'
L
A
A
AL
VL
A I''
V'
V''
I'
I''
1b
A I''
I'
I''
V'I''
V''
AL
V'
A
V
V'
VL
D
I'
3b
4
A
D
L
L
5a
6a
AL
L
MB
D
5b
6b